Bio

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# American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

John D. Mizelle, Editor



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Vol. 48 November, 1952 No. 3

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The following numbers are out of print: Vol. 1 (1, 4, 5, 8-12); Vol. 2 (1-3, 8, 9); Vols. 3, 4 (all numbers); Vol. 5 (1, 6-8); Vol. 6 (1, 5, 7-12); Vol. 7 (1, 6); Vol. 8 (2); Vol. 9 (2); Vol. 11 (1); Vol. 12 (12); Vol. 14 (1, 5-6); Vol. 15 (4); Vol. 16 (2); Vol. 17 (1, 2); Vol. 18 (1); Vol. 20 (1, 2); Vol. 21 (2, 3); Vol. 22 (1); Vols. 23-26 (all numbers); Vol. 27 (1); Vol. 36 (1); Vol. 37 (2, 3); Vol. 38 (1). Volume groups 1-12, 13-18 and 19-44 contain 12, 6 and 3 issues respectively. Available issues of Vols. 1-6 $4.00, single issues 40 cents; Vol. 7 $2.50, single issues 25 cents; Vols. 8-12 $4.00, single issues 40 cents; Vols. 13, 14 $2.50, single issues 50 cents: Vol. 15 $3.00, single issues 60 cents; Vol. 16 $4.00, single issues 75 cents; Vol. 17 $5.50, Part I, $2.50, single issues $1.25. Subscription price per year $6.00.

Inquiries concerning exchanges for specimens, journals, special volumes or duplicate books should be addressed to *The American Midland Naturalist*, Notre Dame, Indiana, where subscriptions and payments are also received. Offers should accompany requests for exchange.

Abbreviated citation: *Amer. Midl. Nat.*

The American Midland Naturalist is indexed in the INTERNATIONAL INDEX.

Entered as second-class matter at Notre Dame, Indiana. Acceptance for mailing at special rate of postage provided for in section 1103; Act of October 3, 1917, authorized on July 3, 1918.

# The American Midland Naturalist

Published Bi-Monthly by The University of Notre Dame, Notre Dame, Indiana

VOL. 48 NOVEMBER, 1952 No. 3

## The Pelvic Musculature of the Loon, Gavia immer[1]

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### Introduction

Birds present a great series of specializations correlated with their habits. Among the most interesting of these specializations are those for swimming and diving. Stresemann (1927-34) points out that many birds are able to swim on the surface of the water, but few are able to dive. In his analysis of diving, he reported that in order to thrust their light bodies under the water some forms make use of the acceleration attained by a steep dive or a free fall from the air. For a true dive of longer duration, in which the body is driven beneath the water under its own power, he found that special construc-

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tion is employed not only in the locomotor, but also in the respiratory apparatus. The extremities push the bird under the water, but they are aided by a device for voluntarily lowering the specific gravity of the body. The true diving birds have very large inspiratory air-sacs which serve this function by being emptied at will. Also their skeletons show a marked decrease in pneumaticity which parallels their increase in diving ability. Consequently, a diving bird with empty air-sacs is much heavier than a non-diver of equal volume.

Stresemann further reported that among diving birds locomotion under the water may be accomplished by use of the legs alone, the legs aided by the wings, or the wings alone. Those birds that use their legs alone, or their legs aided by their wings, move through the water by a series of simultaneous thrusts of both feet. They resemble each other in the general plan of structure of the posterior extremity, but there are outstanding differences in the details of the locomotor apparatus.

The author of this investigation has undertaken to discover the detailed pattern of the pelvic musculature in a highly modified diving bird, and to relate its anatomical features to their functions. The common loon (*Gavia immer*) was selected for this study because it possesses essentially the same pelvic muscles as do the comparatively unspecialized gallinaceous birds. It is a moderately large bird, lending itself well to dissection. Moverover, it is remarkably specialized for swimming and diving, to the extent of being almost totally unable to walk on land. Thus it presents a convenient and interesting subject for a study of the modifications in pelvic musculature which are associated with the peculiarly limited functions of its pelvic appendages.

In the loon the hip-joint is backwardly displaced and the thigh and crus are almost immovably fixed in such a postion as to place the feet far behind the body. The entire thigh and crus are enclosed by the thickly feathered skin of the body wall, a condition made possible by the relatively fixed position of these segments of the leg. Many of the pelvic muscles are attached to the proximal half of the tibia, and the femur and tibia, being joined together by an almost immovable knee-joint, act as a single skeletal unit. Only that part of the leg distal to the intertarsal joint, which is the only portion that projects beyond the body wall, is freely movable. The intertarsal joint is situated at the level of the base of the tail, placing the propelling element behind the body. Shufeldt (1898), reporting his observations on the terrestrial attitude of the loons and grebes, says, ". . . it (the loon) absolutely refused to sit upright, or to assume anything approaching the 'book' attitude attributed to Loons and Grebes. Its method of progression was by little jumps, both feet being moved backward together, the breast never leaving the ground." Although they may do so momentarily ". . . it is the rare exception for either a Loon or a Grebe, when out of water and on *terra firma,* to assume the erect attitude, . . . "

Because its feet are situated behind the body and are incapable of dorsal flexion the loon has difficulty in moving on solid ground. Its development has been directed towards perfection of movement in water, in which the legs are not required to support the weight of the animal, and the movement of the legs and feet is restricted to other planes than those useful in locomotion on land.

The loon, however, swims with ease on the surface of water and even more powerfully beneath it, where the form of his body enables him to pierce the medium with relatively little resistance. The propelling element, situated behind the body, is properly placed to provide efficient power for both swimming and diving.

## Historical

The most outstanding treatise yet published on the pelvic musculature of birds is that of Hudson, in 1937, based particularly on the crow. In it he compared the pelvic myology in the crow with that in representatives of fifteen other orders of North American birds. Many of his findings are in contrast with those reported by Shufeldt (1890b) for the raven. Hudson's work is one of the most carefully prepared and clearly presented papers in the entire field of avian myology. In it he reviews the most important papers which had appeared on that subject up to the date of its publication. The reader is referred to it for an analysis of the older literature. Hudson gave careful study to the five muscles which had been considered valuable in determining relationships of birds and had been used in the myological formula as proposed by Garrod (1873). He proposed a revision of Garrod's formula by adding two other muscles and the vinculum, a tendinous commissure which connects the tendon of M. flexor perforatus digiti III with that of M. flexor perforans et perforatus digiti III.

Three other papers in English on avian myology have appeared since that of Hudson. Howell (1938) presented the results of his efforts to homologize the pelvic muscles of birds with those of reptiles and mammals. Chamberlain (1943) published a descriptive atlas on avian anatomy (myology, arthrology and osteology) based on several species of domestic birds. Fisher (1946) in his paper on New World vultures has presented a scholarly work on the anatomy of that group. This is a splendid study relating form and function in both pectoral and pelvic appendages.

Dabelow (1925) published a paper in which he dealt with the types of locomotion in the various swimming and diving birds, and described the general morphological changes associated with the several types of locomotion. Frank and Neu (1929) reported the results of their detailed studies, made by means of motion pictures and a model of the grebe (*Podiceps*), on the movement of the leg of that bird in swimming.

There exists, therefore, an abundance of published data which are useful as a basis for further work on the pelvic musculature of birds. The works of Dabelow and of Frank and Neu are particularly useful in a study of functional modification of the pelvic muscles of a swimming bird.

## Material

Twenty-five preserved specimens (24 adults and one juvenile) of the common loon (*Gavia immer*) were used in this investigation. The specimens were preserved by injecting 10% formalin with a syringe subdermally, into the larger muscle masses and into the body cavity. The skin and feathers did not interfere with the introduction of the fluid and the preservation of deep structures, and therefore were left intact. After injection, each entire specimen was immersed and stored in a solution of 10% formalin to which a few

crystals of thymol were added to prevent mold. Prior to dissection the specimens were removed from the storage tank, washed in running water, immersed for twelve hours in a curing solution of 1260 gm. of sodium bisulfite and 840 gm. of sodium sulfite to 20 l. of water. The curing solution removed nearly all trace of the odor of formalin and left the specimens firm and in excellent condition for study. The specimens were then washed in running water. To prevent unnecessary drying during dissection only such small sections of skin and feathers were removed as was necessary to expose the area under immediate study. While being studied the specimens were kept moist with embalming fluid (3% phenol, 2% formalin, 20% glycerine, 75% water), and between periods of study they were wrapped in a shroud saturated with this fluid and kept in an air-tight container. Gross dissection with the aid of low power lenses was employed in the investigation.

ACKNOWLEDGEMENTS

Specimens were obtained from the Saginaw Bay area of Michigan through the co-operation of the Institute of Fisheries Research and the Game Division of the Michigan Department of Conservation. The writer wishes to express his gratitude to Dr. A. S. Hazzard and Dr. F. A. Westerman of these organizations for their help in procuring the specimens needed. Especial thanks are due to Officer A. G. Neering for his kindness in collecting and shipping the loons.

The author is deeply indebted to Dr. A. H. Stockard, under whose direction this investigation was made, and to the Museum of Zoology of the University of Michigan and to the Chicago Natural History Museum for making available their collections of skeletal material. Thanks are due to many others of the Biological Station and the Department of Zoology of the University of Michigan for their assistance and encouragement during the course of this study.

## Skeletal Parts

The writer presents here only a brief description of those skeletal parts which will be mentioned in the exposition of the muscles. For a comprehensive description of the skeleton of the loon, the reader is referred to the paper by Coues (1866), which contains a detailed account of the osteology of this bird (under the name *Colymbus torquatus*) and to the works of Shufeldt (1890a and 1904) from which further information may be obtained.

The skeleton of the pelvic girdle and appendage in the loon shows some remarkable specializations. As it is in all birds, the pelvis of the loon (Pl. 12) is firmly anchylosed to the synsacrum and, as it usually is among all aquatic diving birds, is elongate and narrow, its postacetabular portion being twice as long as its preacetabular portion. The pubis is flattened and expanded posteriorly to a greater extent than in most other birds, thus affording greater surface for the attachment of muscles.

The antitrochanter, the surface of the pelvis (Pl. 11) for the articulation of the trochanter of the femur, is large and is situated almost vertically, so that it faces almost directly laterad with little vertical and no axial slope, resembling in these respects the orientation of that surface of *Hesperornis*. The trochanter (Pl. 13) is low on the femur, standing on almost the same level with the capitulum rather than above it, thus allowing the femur to project in the horizontal plane. The femur is almost immovably fixed in this position by bony articulation and the accompanying ligaments. Though its proximal portion is directed horizontally and laterad, perpendicular to the

axis of the trunk, its shaft is strongly curved caudad, enabling the foot to reach the mid-plane behind the body.

Distally the femur articulates with the tibiotarsus and the fibula (Pl. 15), the two bones of the crus. The tibiotarsus likewise lies almost immovably fixed in the horizontal plane, but parallel to the axis of the trunk. Its proximal end bears an anteriorly directed, long, procnemial or rotular process, which represents the elongation of the anterior tibial protuberance of other animals. The rotular process is a place of attachment for the greatly enlarged, primitively extensor muscles of the thigh, and the muscles of the tarsus and toes. On its anterior aspect it bears two conspicuous ridges. These are the anterolateral crest, which extends downward on the shaft of the tibia for one-half of the length of that bone, and the anteromedial crest, which extends downward only to the level of the head of the fibula. Between these two crests lies a deep sulcus for the origin of M. extensor digitorum longus.

The patella is a small, free flake of bone within the common tendon of M. iliotibialis and M. femoritibialis externus. It consists almost entirely of cartilage in some specimens and exhibits at least an outer ring of fibrous cartilage in all. The degree of its ossification may depend upon the age of the specimen, but since there is no method for determining age after the first two years in this species, no correlation of degree of ossification with age was made. The patella lies lateral to the distal end of the femur and the articular notch of the tibia, and therefore takes no part in the formation of the rotular process.

The head of the fibula articulates to the lateral condyle of the femur and to the lateral aspect of the head of the tibia. The fibula and tibiotarsus are firmly united in several places by ligamentous anchyloses which permit little rotation between them, though slight rotation of the two of them on the distal end of the femur is possible.

Distally the tibiotarsus articulates with the tarsometatarsus, commonly known in birds as the "tarsus," which supports the three elongated anterior digits (II, III, and IV), and the hallux (I) with its small, sickle-shaped, free metatarsal. Near the proximal end and on the posterior aspect of the tarsometatarsus is a prominent bony canal, covered by a bridge formed from an elevation of the lateral ridges of the posterior sulcus, which lies beneath the area of insertion of the tendon of the gastrocnemius muscle. This bridge, which Coues (1866) has named the *os calcis,* encloses the flexor tendons of the digits.

## Nomenclature of Muscles

The terminology of the muscles used in this work is based for the most part upon that used by Hudson (1937). This was done to avoid adding to the confusion of nomenclature already in existence. An exception is the name *M. extensor hallucis longus* of Hudson, which in this paper is called *M. extensor hallucis.* This muscle is very small in the loon, and is confined to the region of the hallux and its supporting metatarsal. It is the only known extensor for the hallux in any bird, and its homology with muscles in other forms has not been determined. There is, therefore, no reason at this time for labelling it a *long extensor.* If a descriptive term is needed at all, *short* or *brevis* would be more appropriate.

The names of muscles are latinized and therefore in this work *M. tibialis anterior* of Hudson becomes *M. tibialis anticus,* and *anticus* and *posticus* replace *anterior* and *posterior,* respectively, in the names of Mm. iliotrochanterici. *Peronaeus* of Hudson is shortened to *peroneus* in accordance with current usage.

The following pages contain a table of synonymy in which the terminology for the muscles of the pelvic girdle and appendage used by various authors is listed. The terminology used by Hudson (1937) is here compared to that of Watson (1883), Shufeldt (1890b) and Gadow and Selenka (1891). The publications of these last three are the most complete works which appeared prior to Hudson's publication. The terminology of Stolpe (1932), who published five years before Hudson and followed very closely the terminology of Gadow, is also listed. In addition, the terminology employed in each of the two papers that have appeared in English since Hudson's work was published, namely that of Howell (1938) and Chamberlain (1943), is listed. Fisher (1946) has derived his nomenclature from largely the same sources and the reader is referred to Table 42 of his paper for his table of synonymy.

The names used for the nerves are still somewhat confusing. Those used in this paper are based on the names used by Gadow and Selenka (1891) and Watson (1883), and will differ from those used by Fisher. Further study on the lumbo-sacral plexus is needed to clarify the exact make-up and distribution of the fibers involved.

### NOMENCLATURE OF MUSCLES USED BY VARIOUS AUTHORS

a. Hudson (1937), b. Watson (1883), c. Howell (1938), d. Gadow (1891), e. Shufeldt (1890b), f. Chamberlain (1943), g. Stolpe (1932).

1. a. Abductor digiti II, b. Abductor digiti interni, d. Abductor digiti II, f. Extensor digiti brevis (part).

2. a. Abductor digiti IV, b. Abductor digiti externus, d. Abductor digiti IV, f. Interossei.

3. a. Adductor digiti II, d. Adductor digiti II, f. Interossei.

4. a. Adductor digiti IV, b. Adductor digiti externus, d. Adductor digiti IV.

5. a. Adductor longus et brevis, b. Adductor magnus, c. Adductor superficialis & profundus, d. Pub-ischio-femoralis, e. Adductor longus & Adductor magnus, f. Adductor, g. Pub-ischio-femoralis.

6. a. Ambiens, b. Ambiens, c. Ambiens, d. Ambiens, f. Pectineus (Ambiens).

7. a. Biceps femoris, b. Biceps femoris, c. Extensor ilio-fibularis, d. Ilio-fibularis, e. Biceps flexor cruris, f. Semitendinosus, g. Ilio-fibularis.

8. a. Extensor brevis digiti IV, d. Extensor brevis digiti IV, f. Extensoris digiti brevis (part).

9. a. Extensor digitorum longus, b. Extensor communis digitorum, d. Extensor digitorum communis, e. Extensor longus digitorum, f. Extensor digitus longus, g. Extensor digitorum communis.

10. a. Extensor hallucis longus, b. Extensor brevis hallucis, d. Extensor hallucis brevis, e. Extensor hallucis brevis, f. Extensor hallucis brevis.*

11. a. Extensor proprius digiti III, b. Extensor proprius digiti medii, d. Extensor proprius digiti III.

12. a. Femori-tibialis externus, b. Extensor cruris (part), c. Femorocrural extensor,

* Mentioned on Chamberlain's plates but not in his text.

vastus lateralis, d. Femori-tibialis externus, e. Extensor femoris, vastus externus, f. Tensor fascia latae, g. Femoro-tibialis externus.

13. a. Femori-tibialis internus, b. Gracilis, c. Femorocrural extensor, vastus medialis, d. Femori-tibialis internus, e. Extensor femoris, cruraeus, f. Quadriceps femoris, vastus medius.

14. a. Femori-tibialis medius, b. Extensor cruris (part), c. Femorocrural extensor, d. Femori-tibialis medius, e. Vastus internus, f. Rectus femoris, g. Femoro-tibialis medius.

15. a. Flexor digitorum longus, b. Flexor perforans digitorum (part), d. Flexor profundus s. perforans, e. Flexor perforans digitorum profundus, f. Flexor digitus perforans.

16. a. Flexor hallucis brevis, b. Flexor hallucis brevis, d. Flexor hallucis brevis, e. Flexor brevis hallucis, f. Flexor hallucis brevis.

17. a. Flexor hallucis longus, b. Flexor perforans digitorum (part), d. Flexor hallucis longus, e. Flexor longus hallucis, f. Flexor hallucis longus.

18. a. Flexor perforans et perforatus digiti II, b. Flexor perforatus et perforans digiti interni, d. Flexor perforans et perforatus digiti II, e. Flexor perforatus indicis secundus pedis, f. Flexor digitus perforatus et perforans digiti secundi digit.

19. a. Flexor perforans et perforatus digiti III, b. Flexor perforatus et perforans digiti medii, d. Flexor perforans et perforatus digiti III, e. Flexor perforatus medius secundus pedis, f. Flexor digitus perforatus et perforans digiti terti.

20. a. Flexor perforatus digiti II, b. Flexor perforatus digiti internus, d. Flexor perforatus digiti II, e. Flexor perforatus primus pedis, f. Flexor digitus perforatus digiti secundi.

21. a. Flexor perforatus digiti III, b. Flexor perforatus digiti medii, d. Flexor perforatus digiti III, e. Flexor perforatus medius primus pedis, f. Flexor digitus perforatus digiti terti.

22. a. Flexor perforatus digiti IV, b. Flexor perforatus digiti externi, d. Flexor perforatus digiti IV, e. Flexor perforatus annularis primus pedis, f. Flexor digitus perforatus digiti quartus.

23. a. Gastrocnemius, b. Gastrocnemius, d. Gastrocnemius, e. Gastrocnemius, f. Gastrocnemius, g. Gastrocnemius.

24. a. Gluteus medius et minimus, c. Piriformis, d. Ilio-femoralis externus, f. Gluteus superficialis (caudal part), g. Ilio-femoralis.

25. a. Iliacus, b. Pectineus, c. Psoas, d. Ilio-femoralis internus, f. Iliacus.

26. a. Ilio-tibialis, b. Rectus femoris & Tensor fascia femoris, c. Extensor iliotibialis lateralis, d. Ilio-tibialis, e. Gluteus primus, f. Biceps femoris, g. Ilio-tibialis posterior.

27. a. Ilio-trochantericus anterior, b. Gluteus minimus, c. Iliacus, d. Ilio-trochantericus anterior, e. Gluteus minimus, f. Gluteus superficialis (cranial part), g. Ilio-trochantericus.

28. a. Ilio-trochantericus medius, d. Ilio-trochantericus medius, f. Gluteus profundus, g. Ilio-trochantericus.

29. a. Ilio-trochantericus posterior, b. Gluteus medius, c. Gluteus profundus, d. Ilio-trochantericus posterior, e. Gluteus medius, f. Gluteus medius, g. Ilio-trochantericus.

30. a. Ischio-femoralis, b. Obturator externus, c. Flexor ischiofemoralis, d. Ischio-femoralis, e. Obturator externus, f. ? (Quadratus femoris), g. Ischio-femoralis.

31. a. Obturator externus, b. Gemellus, c. Obturator (part), d. Accessorii M. obturator, e. Gemellus, f. Gemelli.

32. a. Obturator internus, b. Obturator internus, c. Obturator (part), d. Obturator, e. Obturator internus, f. Obturator internus, g. Obturator.

33. a. Peronaeus brevis, b. Peroneus brevis, d. Peroneus profundus, e. Tibialis posticus, f. Peroneus tertius, g. Peroneus profundus.

34. a. Peronaeus longus, b. Peroneus longus, d. Peroneus superficialis, e. Peroneus longus, f. Peroneus longus, g. Peroneus superficialis.

35. a. Piriformis pars caudo-femoralis, b. Cruro-coccygeal, c. Caudo-femoralis, d. Caud-ilio-femoralis (part), e. Femoro-caudal, f. Cruratis caudalis, g. Caud-ilio-femoralis (part).

36. a. Piriformis pars ilio-femoralis, b. Adductor longus femoris, c. Flexor ilio-

femoralis, d. Caud-ilio-femoralis (part), f. Quadratus femoris, g. Caud-ilio-femoralis (part).

37. a. Plantaris, b. Plantaris, d. Plantaris, e. Soleus, f. Tibialis caudalis.*

38. a. Popliteus, b. Popliteus, d. Popliteus, f. Popliteus.

39. a. Sartorius, b. Sartorius, c. Extensor iliotibialis anterior, d. Ilio-tibialis internus s. sartorius, e. Sartorius, f. Sartorius, g. Ilio-tibialis anterior.

40. a. Semimembranosus, b. Semimembranosus, c. Flexor cruris medialis,** d. Ischio-flexorius, e. Semimembranosus, f. Gracilis, g. Ischio-flexorius.

41. a. Semitendinosus, b. Semitendinosus, c. Flexor cruris lateralis,*** d. Caud-ilio-flexorius, e. Semitendinosus, f. Semimembranosus, g. Caud-ilio-flexorius.

42. a. Tibialis anterior, b. Tibialis magnus, d. Tibialis anticus, e. Tibialis anticus, f. Tibialis cranialis, g. Tibialis anticus.

## Description of Pelvic Muscles

### Musculus Iliotibialis

*Form and position:* M. iliotibialis (Pls. 2-12, 16, 26) is the most conspicuous muscle seen on the dorsal aspect of the hip after removal of the skin. In position it is superficial, and in form it resembles the trapezius of man in that with its mate of the other side, from which it is separated only by the extreme dorsum of the dorsal spinal crests and covering fascia, it forms a trapezoid. It is a broad triangular muscle which arises from the dorsal spinal crests of the last two dorsal and the fused sacral vertebrae as far back as the level of the posterior margin of the ischiatic foramen, and from a muscular ridge of the ilium which extends from a level with the anterior border of the acetabulum caudad for a distance equal to three-fourths of the length of the ischiatic foramen. The anterior one-fifth and the posterior one-third of its origin are fleshy, while the central portion of its origin is aponeurotic. The anterior porton of the muscle is much thinner than is its posterior portion. Its anterior fibers run obliquely caudolaterad, its middle fibers run directly laterad, and its posterior fibers run obliquely craniolaterad, all converging laterad to form a broad tendinous sheet whose ventral surface is fused with the dorsal surface of a similar tendinous sheet formed by M. femoritibialis externus. This common tendon passes directly over the lateral (dorsal) surface of the knee-joint to insert on the lateral crest of the articular notch of the tibiotarsus.

*Relations:* Anteriorly M. iliotibialis is bordered by the superficial anterior third of M. sartorius, and posteriorly by the superficial portions of M. biceps femoris and the external head of M. gastrocnemius. It completely covers the underlying Mm. iliotrochanterici, M. femoritibialis externus, and the proximal portion of M. femoritibialis medius. Its tendon of insertion, which is fused to that of the underlying tendon of M. femoritibialis externus passes between the external head of M. gastrocnemius and M. flexor perforans et perforatus digiti II. The tendon, as it passes over the lateral (dorsal) surface of the knee-joint, contains a thin sesamoid bone, the patella. The tendon of M. ambiens makes its appearance on the lateral side just above the knee-joint and in coursing caudad extends over (lateral to) the patellar tendon.

*Action:* Contraction of the entire M. iliotibialis abducts the thigh and at the same time rotates the leg dorso-mesiad. The anterior fibers are antagonistic to M. sartorius and when contracting alone extend the crus slightly. On the other hand, contraction of the heavy posterior fibrous portion alone of the muscle flexes the crus to a slight extent.

*Nerve supply:* M. iliotibialis is supplied by a branch of the anterior crural nerve.

### Musculus Sartorius

*Form and position:* M. sartorius (Pls. 2-12, 16, 26) arises fleshily from the dorsum of the neural spines of the second and third from the last dorsal vertebrae (anterior by one to the fused sacral vertebrae) and from the extreme cranial end and the anterior half of the ventrolateral margin of the preacetabular portion of the ilium. Its fibers run

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* M. tibialis posterior on Chamberlain's plates.

** M. semitendinosus on Howell's plates.

*** M. biceps on Howell's plates.

obliquely caudolaterad to their insertion on the basal half of the mesial aspect of the rotular process of the tibia.

*Relations:* The proximal portion of the anterior third of this muscle is superficial and lies in front of the anterior margin of M. iliotibialis, while the posterior two-thirds of its proximal portion is covered by the anterior fibers of M. iliotibialis. Its distal portion, which is covered by M. femoritibialis medius, in turn covers the narrow tendon of M. ambiens as it turns laterad (primitively dorsad) to penetrate the muscles on the mesial aspect of the knee-joint.

*Action:* Upon contracting, M. sartorius protracts the thigh and crus and slightly rotates the crus ventromesiad, thus abducting the crus and supinating the foot.

*Nerve supply:* A branch of the anterior crural nerve supplies M. sartorius.

### MUSCULUS ILIOTROCHANTERICUS POSTICUS

*Form and position:* M. iliotrochantericus anticus (Pls. 3, 4, 7-12, 14, 26), a muscle a head which is broad, and on the bony surface to which it attaches it forms an obtuse triangle whose greatest angle is ventral and whose smallest angle is anterior. The thin anterior portion of its head is attached by an aponeurosis to the neural spines of the two most anterior of the fused sacral vertebrae and to the tendons of M. semispinalis dorsi. Its posterior portion arises by a fleshy attachment from the lateral aspect of M. semispinalis dorsi and from the dorsal third of the lateral aspect of the preacetabular fossa of the ilium, the origin of this portion extending caudad as far as the anterosuperior margin of the acetabulum. The anterior fibers of this muscle slant sharply caudolaterad, while its posterior fibers run laterad. All of its fibers converge into a broad insertion on the anterior superior ridge of the lateral aspect of the trochanter of the femur, immediately mesial to the lateral aponeurotic head of the M. femoritibialis externus.

*Relations:* M. iliotrochantericus posticus is one of a group of muscles lying deep to M. iliotibialis. Its entire dorsal and lateral aspects are covered by the anterior and middle portions of the latter. Its anterior margin is separated from the posterior margin of M. iliotrochantericus anticus by a tendinous sheet from which some fibers of each of these muscles arise. Posteriorly this muscle is bordered by the anterior margin of M. gluteus medius et minimus.

*Action:* M. iliotrochantericus posticus rotates the femur craniomesiad and consequently elevates or abducts the more distal elements of the leg.

*Nerve supply:* M. iliotrochantericus posticus is supplied by a branch of the anterior crural nerve.

### MUSCULUS ILIOTROCHANTERICUS ANTICUS

*Form and position:* M. iliotrochantericus anticus (Pls. 3, 4, 7-12, 14, 26), a muscle which is fleshy almost throughout, arises from the anterior and ventral portions of that part of the ilium anterior to the acetabulum. Its origin extends caudad to a point about one centimeter in front of the acetabulum, where the lateral surface of the ilium twists from a horizontal to a nearly vertical plane. Its fibers run caudolaterad to insert by a short, relatively heavy tendon on the anterolateral ridge of the femur just distal to the articular surface of the trochanter.

*Relations:* M. iliotrochantericus anticus lies deep to M. iliotibialis in the space among M. iliotrochantericus posticus, M. sartorius and M. femoritibialis medius. Its posterior margin lies along the tendon from which some of its fibers and those for M. iliotrochantericus posticus arise, and fibers of the latter partially cover its dorsomesial surface. Its insertion is on the femur just distal to that of M. iliotrochantericus medius.

*Action:* This muscle rotates the femur craniomediad and aids in abduction of the femur.

*Nerve supply:* A branch of the anterior crural nerve supplies M. iliotrochantericus anticus.

### MUSCULUS ILIOTROCHANTERICUS MEDIUS

*Form and position:* M. iliotrochantericus medius (Pls. 4-6, 11, 12, 14, 26) arises from the ventral margin of the posterior one-third of the preacetabular portion of the ilium and inserts on the anterolateral intermuscular ridge just distal to the trochanter of the femur. It is fleshy throughout, and roughly pyramidal in shape, its fleshy origin forming the base and its insertion forming the apex of the pyramid.

*Relations:* M. iliotrochantericus medius lies deep to M. iliotrochantericus posticus and posterior to M. iliotrochantericus anticus. It is entirely concealed by the former and completely fills the space between the posterior border of the latter and the neck of the femur. Its insertion lies between the insertions of the other two iliotrochanterici.

*Action:* M. iliotrochantericus medius rotates the dorsal (primitively lateral) surface of the femur craniad.

*Nerve supply:* This muscle receives its nerve supply from a branch of the anterior crural nerve.

### Musculus Gluteus Medius et Minimus

*Form and position:* M. gluteus medium et minimus (Pls. 3-6, 11, 12, 14, 26) is a very small muscle arising from the aponeurotic sheet between the neural crest of the fused sacral vertebrae and the dorsal margin of the ilium dorsal to the acetabulum. Its fibers run laterad and insert on the posterior margin of the trochanter of the femur.

*Relations:* The anterior margin of the muscle is intimately associated with the posterior border of M. iliotrochantericus posticus. It lies deep to and is entirely covered by the middle fibers of M. iliotibialis. Its insertion is on the posterior margin of the trochanter at the same level as that of M. obturator internus.

*Action:* M. gluteus medius et minimus is a weak abductor of the femur.

*Nerve supply:* A branch of the anterior crural nerve supplies this muscle.

### Musculus Biceps Femoris

*Form and position:* M. biceps femoris (Pls. 2-6, 11, 12, 16, 26) is a broad single-headed muscle which arises from the dorsal crests of the spines of the fused sacral vertebrae and from the area which extends caudad from the posterior margin of M. iliotibialis to a point half-way between the posterior border of the ischiatic foramen and the tip of the posterior iliac spine. Its origin also includes the dorsal ridge of the postacetabular portion of the ilium and the lateral surface of the ilium immediately below that ridge, from the level of the middle of the ischiatic foramen to as far caudad as the base of the posterior iliac spine. From their origin the fleshy fibers of its middle and posterior portions pass laterad to form a broad tendon whose fibers turn sharply craniolaterad to meet the fibers of the anterior portion. From here they continue laterad with the latter fibers and converge into a narrow tendon which passes through the supporting tendinous loop to insert on the bicipital tubercle of the fibula.

*Relations:* This muscle is only partially superficial. Its anteroproximal end is covered by the caudal portion of M. iliotibialis and its tendinous portion is covered by the external head of M. gastrocnemius. Its tendon passes between the external head of M. gastrocnemius and M. flexor perforatus digiti IV. This narrow tendon passes laterad to its insertion, and is pulled craniad by a loop of tendinous fibers, the biceps loop (Plate IV), which produces in it a bend of about 45°. The biceps loop is formed by three arms, two from the femur and one from the crus. The femoral arms, a proximal and a distal, arise from the posterolateral aspect of the shaft of the femur along with the fibers of the external head of M. gastrocnemius, with which they are intimately associated and from which they probably were derived. The proximal arm passes mesial to the tendon of M. biceps femoris, and the distal arm runs lateral to it. The caudal end of the distal arm is connected to the crural arm. M. flexor hallucis longus is attached to the tendinous sheet formed by the crural arm, and the sheet is covered externally by the belly of M. flexor perforans et perforatus digiti II. This crural arm prevents adduction of the biceps loop during contraction of M. biceps femoris.

*Action:* M. biceps femoris adducts the crus and rotates it slightly laterad.

*Nerve supply:* M. biceps femoris is innervated by a branch of the ischiatic nerve.

### Musculus Ischiofemoralis

*Form and position:* M. ischiofemoralis (Pls. 3-6, 10-12, 14, 26) is a short, cylindrical, semitendinous muscle whose fibers arise along the dorsal, posterior and ventral margins of the ischiatic foramen. The area of its origin extends along one-fourth of the length of the dorsal margin and three-fourths of the length of the ventral margin of the foramen, as well as over the ligament covering the posterior third of the foramen. Poste-

rior to the foramen the area of origin covers the entire two-fifths of the flat plate formed by the fusion of the ilium and the ischium. The lateral surface of this muscle is covered by a heavy tendinous sheet into which underlying fleshy fibers are inserted, and only along its dorsal margin do any of its fleshy fibers overlie this sheet. Its fleshy fibers extend craniad to insert on the posterolateral aspect of the femur along with the insertions of Mm. obturator internus and Mm. obturator externus, and opposite the insertions of the three Mm. iliotrochanterici.

*Relations:* The origin of M. ischiofemoralis is covered by the anterior portion of M. biceps femoris and M. piriformis pars iliofemoralis. Ventrally it is in contact with the anterior half of the dorsal surface of the origin of M. semimembranosus.

*Action:* This muscle rotates the thigh caudad, acting as an antagonist of the three iliotrochanteric muscles.

*Nerve supply:* M. ischiofemoralis receives a branch of the obturator nerve.

### MUSCULUS PIRIFORMIS

*Form and position:* M. piriformis (Pls. 2-12, 14, 26) consists of two parts, pars iliofemoralis and pars caudofemoralis. Pars iliofemoralis is a powerful muscle arising by a broad apoenurosis attached to the dorsal ridge of the postacetabular portion of the ilium, and by fleshy fibers from the entire lateral surface of the postacetabular portion of the ilium as far caudad as the base of the posterior iliac process, from the lateral surface of the ischium immediately below the postacetabular portion of the ilium, and from the dorsolateral surface of the posterior iliac process. Due to the presence on its dorsolateral aspect of a broad tendinous sheet to which its fleshy fibers are firmly attached, this muscle appears tendinous. Its main portion, however, is fleshy. Its fibers run cranioventrolaterad to insert on the posterior aspect of the shaft of the femur along a ridge beginning on the lateral margin of the posterior surface midway down the shaft and running obliquely mesiad to a point on the mesial margin of the shaft about three-fourths of the way down. To the posterolateral margin of its broad tendon, the slender tendon of pars caudofemoralis is attached.

Pars caudofemoralis is a very long and slender strand which arises fleshily from the ventrolateral aspect of the transverse processes of the coccygeal vertebrae and runs craniad. It soon passes into a long slender tendon which fuses with the tendon of pars iliofemoralis, and finally inserts on the posterior aspect of the shaft of the femur.

*Relations:* The middle portion of pars iliofemoralis lies beneath M. biceps femoris, while its posterior portion is superficial behind the caudal margin of that muscle. Ventrally it is in contact with M. semimembranosus, and at the posterior iliac process its origin lies immediately dorsal to the origin of M. semitendinosus. The long tendon of pars caudofemoralis extends between M. piriformis pars iliofemoralis and M. semitendinosus. The insertion of M. piriformis, on the posterior aspect of the shaft of the femur, is bounded mesially by the insertion of M. adductor longus et brevis and laterally by the origin of Mm. flexori perforati digiti III and IV.

*Action:* The entire muscle retracts the femur. If the femur is fixed, pars caudofemoralis flexes the tail laterad.

*Nerve supply:* The ischiatic nerve contributes fibers to both parts of M. piriformis, and also the anterior coccygeal nerve sends fibers to pars caudofemoralis.

### MUSCULUS SEMITENDINOSUS

*Form and position:* M. semitendinosus (Pls. 2-6, 8, 9, 11, 12, 16, 26) arises fleshily from the tip and the ventrolateral surface of the posterior iliac process. It also receives a slip from the tendinous origin of M. transversoanalis. Its fibers run craniolaterad and form a thin tendon which fuses with the posterolateral side of the broad tendon of M. semimembranosus, the fused tendons of these two muscles inserting on the posteromesial surface of the tibiotarsus.

*Relations:* M. semitendinosus lies ventrolateral to M. piriformis pars iliofemoralis, their origins being separated only by the lateral crest of the posterior iliac spine.

*Action:* M. semitendinosus retracts the crus and rotates it slightly mesiad.

*Nerve supply:* Innervation is supplied by a branch from the ischiatic nerve.

### Musculus Semimembranosus

*Form and position:* M. semimembranosus (Pls. 8, 9, 11, 12, 16, 26) arises as a broad, fleshy sheet from the middle third of the dorsolateral face of the ischium immediately below the origins of M. ischiofemoralis and M. piriformis pars iliofemoralis. The muscle extends laterad, forming a broad thin tendon of M. semitendinosus. The common tendon of these two muscles inserts on the posteromesial surface of the proximal half of the tibiotarsus along a line parallel to its axis.

*Relations:* M. semimembranosus separates M. adductor longus et brevis from M. piriformis, the latter completely covering the dorsal aspect of its proximal half. Distally M. semimembranosus and M. semitendinosus pass between the internal head and the medial head of M. gastrocnemius.

*Action:* M. semimembranosus flexes and adducts the crus and rotates it slightly mediad.

*Nerve supply:* M. semimembranosus is innervated by a branch of the ischiatic nerve.

### Musculus Adductor Longus et Brevis

*Form and position:* M. adductor longus et brevis (Pls. 7-9, 11, 12, 14, 26) arises in a line along the entire ventrolateral margin of the ischium, from the ischiopubic ligament, and from the dorsolateral margin of the postacetabular portion of the pubis to as far back as its ligamentous junction with the caudal tip of the ischium. Its fleshy fibers run craniad to the femur where they insert as two separate slips which are separated by a hiatus through which pass the femoral vessels of the leg. The proximal slip inserts on the posteromesial surface of the femur along a narrow line which begins at the tubercle for the insertion of M. piriformis and extends proximad to a point half the distance up the femoral shaft. The distal slip inserts along a line which begins on the posteriomesial aspect of the medial condyle of the femur and continues proximad as far as the tubercle for the insertion of M. piriformis. The proximal slip represents M. adductor brevis and the distal slip represents M. adductor longus of other tetrapods.

*Relations:* M. adductor longus et brevis is superficial on the mesial aspect of the thigh. Its dorsal surface is in contact with Mm. semimembranosus, semitendinosus, and piriformis, and the medial head of M. gastrocnemius.

*Action:* The adductor longus et brevis retracts the thigh and the entire leg, and rotates the thigh slightly craniomesiad so as to elevate the leg.

*Nerve supply:* It receives a branch of the obturator nerve.

### Musculus Obturator Internus

*Form and position:* The fleshy fibers of M. obturator internus (Pls. 3-10, 12, 14, 26) take their origin along grooves on the dorsomesial surface of the postacetabular pubic process and on the ventromesial margin of the ischium, as well as over almost the entire mesial surface of the ischiopubic ligament. A central tendon is formed along the lateral surface of the muscle, and as the muscle passes to the lateral surface of the pelvis through the open anterior end of the obturator foramen, the remainder of the foramen being closed by the ischiopubic ligament, the tendon partially ensheathes its mesial fleshy fibers. It inserts on a tubercle on the proximocaudal angle of the lateral aspect of the trochanter of the femur.

*Relations:* M. obturator internus occupies the space between the ischium and the pubis on the mesial surface of the pelvis. Its shape corresponds to that of the obturator foramen. It is separated from the deep muscle of the lateral aspect of the pelvis by the heavy ligamentous sheet which closes the obturator foramen over nearly its entire length.

*Action:* M. obturator internus rotates the head of the femur caudad, thus aiding in depressing the entire leg ventrad.

*Nerve supply:* This muscle is supplied by a branch of the obturator nerve which accompanies it through the anterior end of the obturator foramen.

### MUSCULUS OBTURATOR EXTERNUS

*Form and position:* M. obturator externus (Pls. 10-12, 14, 26) arises from the area between the anterior end of the obturator foramen and the aectabulum. This postacetabular area is the site of the junction of the ischium with the pubis. The fibers of the muscle inserts on the tubercle on the posterior margin of the trochanter of the femur.

*Relations:* At its insertion the fibers of M. obturator externus are so closely applied to those of M. obturator internus that separation is difficult.

*Action:* M. obturator externus rotates the head of the thigh caudad, and so aids in depressing the distal segments of the leg.

*Nerve supply:* This muscle receives a branch of the obturator nerve immediately after that nerve reaches the lateral aspect of the pelvis.

### MUSCULUS ILIACUS

*Form and position:* M. iliacus (Pls. 7-12, 14, 26) is a very short, fleshy muscle whose fibers arise from the ventral margin of that portion of the ilium immediately anterior to the acetabulum. Its fibers run caudolaterad to insert on a tubercle on the mesial aspect of the base of the neck of the femur, just distal to the head.

*Relations:* M. iliacus is a deep muscle which is best seen from a mesial or ventral view of the thigh and pelvis. Its origin lies deep and ventral to that of M. iliotrochantericus medius. Its insertion, on the base of the neck of the femur, is bounded on three sides by the fibers of the head of M. femoritibialis internus.

*Action:* M. iliacus rotates the head of the femur slightly craniolaterad and adducts the appendage slightly.

*Nerve supply:* The crural nerve supplies this muscle.

### MUSCULUS AMBIENS

*Form and position:* M. ambiens (Pls. 5-12, 26) is a broad, thin sheet of muscle arising by very short tendinous slips from the spinous process and the subacetabular portion of the pubis. Its fibers run laterad parallel to the femur, and the muscle tapers sharply to form a narrow tendon near the distal end of the femur. This tendon makes a right turn dorsad to penetrate the overlying mass of Mm. femoritibialis medius and femoritibialis internus, and reaches the posterior margin of the rotular process of the tibia. Here, in an oblique groove (Plate 15) whose lower lip is upturned to support it, the tendon of M. ambiens extends to the dorsal (lateral) aspect of the knee-joint, where it emerges between the patellar tendon and the caudal point of insertion of M. femoritibialis medius. The tendon turns caudad, crosses over the patellar tendon, and extends into the aponeurotic sheet from which the flexor muscles of the toes take at least a part of their origin.

*Relations:* The fleshy part of M. ambiens lies on the ventral or mesial aspect of the thigh, where it is covered dorsally by M. femoritibialis internus. Its tendon penetrates between the distal fibers of M. femoritibialis internus and M. femoritibialis medius to reach the ambiens groove on the posterior aspect of the rotular process. At its point of emergence on the lateral (dorsal) side of the knee-joint, this tendon is covered by the belly of M. flexor perforans et perforatus digiti III, and lies just posterior to the intermuscular septum from which most of the fibers of the latter muscle arise. The ambiens tendon lies mesial to the tendon of M. biceps femoris.

*Action:* M. ambiens aids in adduction or medial rotation of the thigh.

*Nerve supply:* It is innervated by a branch from the crural nerve.

### MUSCULUS FEMORITIBIALIS EXTERNUS

*Form and position:* M. femoritibialis externus (Pls. 3-6, 14, 16, 26) arises from most of the lateral surface of the femur. Its most proximal fibers arise on the trochanter between the ridge for the insertion of Mm. iliotrochantericus anticus and iliotrochantericus posticus and that of M. ischiofemoralis. The remainder of its origin extends distad over almost the entire lateral aspect of the shaft of the femur, as far as the external condyle. A short distance above the external condyle the muscle becomes tendinous, and

is joined on its external surface by the overlying tendinous fibers of M. iliotibialis, and on its cranial surface by fibers from M. femoritibialis medius, to form the "patellar tendon." This tendon, containing the patella, passes directly over the lateral surface of the knee-joint and inserts on the lateral crest of the articular notch of the tibia.

*Relations:* M. femoritibialis externus is entirely covered by the middle portion of M. iliotibialis. Anteriorly its fibers are in such close contact with those of the lateral edge of M. femoritibialis medius that separation of these two muscles along this line is difficult. Caudally it is bounded by the proximal portion of the lateral head of M. gastrocnemius. At its proximal end the cranial portion of the narrow head of this muscle lies between the insertions of the two iliotrochanteric muscles, and its caudal portion lies among M. ischiofemoralis, M. obturator internus and M. obturator externus.

*Action:* M. femoritibialis externus rotates the crus laterad.

*Nerve supply:* A branch of the crural nerve supplies this muscle.

### MUSCULUS FEMORITIBIALIS MEDIUS

*Form and position:* M. femoritibialis medius (Pls. 2-10, 14, 16, 26) is a very heavy and powerful triangular muscle which is fleshy throughout. It arises from the neck and the anterior aspect of the entire shaft of the femur. The proximal end of its head completely covers the anterior surface of the neck of the femur and base of the trochanter. The area of its origin follows a narrow line along the shaft of the femur between the origins of M. femoritibialis internus and M. femoritibialis externus, and then broadens at the distal end of the femur to cover the intercondyloid area. Its insertion is on the entire posterior aspect of the rotular process of the tibia, except for the diagonal groove in which the ambiens tendon lies. Its insertion also covers a small area on the mesial surface of the superior half of the rotular process.

*Relations:* M. femoritibialis medius occupies the anterior aspect of the thigh. Its proximal third is covered by the anterior portion of M. iliotibialis; its middle third is superficial, passing lateral to the distal half of M. sartorius, from which it is separated by a fatty fascia; and its distal third is deep, running mesial to M. flexor perforans et perforatus digiti II and M. flexor perforans et perforatus digiti III. The origins of Mm. femoritibialis medius and femoritibialis externus are separated proximally by the insertions of Mm. iliotrochantericus anticus and iliotrochantericus medius, while throughout the rest of the extent of their origins they are so closely in contact with one another that their fibers interdigitate. This is especially true at the distal end, where it is difficult to separate them.

*Action:* M. femoritibialis medius produces slight extension and slight lateral rotation of the crus on the femur.

*Nerve supply:* M. femoritibialis medius is supplied by a branch of the crural nerve.

### MUSCULUS FEMORITIBIALIS INTERNUS

*Form and position:* M. femoritibialis internus (Pls. 6, 8-10, 14, 16, 26) arises from almost the entire anteromesial surface of the femur. Its proximal end is forked around the base of the femur and its anterior border extends onto the anterior surface of the shaft of the femur under the mesial fibers of M. femoritibialis medius. Near the distal end of the shaft of the femur the fibers of these two muscles are rather closely united. The insertion of M. femoritibialis internus is on that part of the mesial aspect of the tibia which lies immediately in front of the mesal lip of the tibial notch (knee-joint).

*Relations:* The proximal end of the head of M. femoritibialis is forked about the base of the neck of the femur in such a way as to allow M. iliacus to pass between the limbs of its fork and insert on the tubercle at the base of the neck of the femur. The cranial border of M. femoritibialis internus is in close contact with the medial margin of M. femoritibialis medius, its posterior border is bounded by the insertions of M. adductor longus et brevis and M. piriformis, while its ventral (mesial) portion is covered by M. ambiens.

*Action:* Mesial rotation of the crus is produced by the M. femoritibialis internus.

*Nerve supply:* This muscle receives a branch of the crural nerve.

## MUSCULUS TIBIALIS ANTICUS

*Form and position:* M. tibialis anticus (Pls. 2-10, 14, 16, 17, 24, 26) arises by two heads, a lateral and a mesial. The mesial head arises from the tip of the anterior surface of the rotular process of the tibiotarsus. Its fibers occupy the deep groove on the rotular process for about 1.5 cm. below the tip, where the groove is then occupied by the deeper M. extensor digitorum longus. The fibers of M. tibialis anticus are then crowded out to sides of the groove. Mesially the fibers arise along the anteromedial crest of the tibia for more than half of its length. Laterally its fibers arise along the anterolateral crest of the tibia down to the level of the head of the fibula. The lateral head of M. tibialis anticus arises as a strong tendon from a tubercle on the anterior surface of the lateral condyle of the femur. The fibers of the two heads unite immediately below the knee-joint and form a strong cylindrical muscle which merges into a strong tendon just above the condyles of the tibiotarsus. At this point the tendon is held in place by a transverse fibrous ligament. The tendon then continues down in the anterior intercondyloid space as the considerably flattened, superficial tendon, which widens as it crosses the tarsal joint, and inserts on a divided tubercle on the anterior surface of the tarsometatarsus immediately below the two malleoli. Fibers from the mesial and the superficial aspects of the inserting tendon continue on down the shaft of the tarsometatarsus to form a heavy aponeurotic sheath which binds the underlying tendon of M. extensor digitorum longus in its canal.

*Relations:* M. tibialis anticus is covered superficially by M. peroneus longus, and is lateral to the lateral origin of M. flexor perforans et perforatus digiti II. The mesial head of M. tibialis anticus ensheathes the deeper-lying M. extensor digitorum longus. The lateral head of M. tibialis anticus is crossed by the tendon of M. ambiens.

*Action:* This muscle effects strong dorsal flexion of the tarsometatarsus. At the same time that it flexes the tarsus dorsad, because of the contour of the proximal end of the tarsometatarsus it also rotates the tarsus ventromesiad.

*Nerve supply:* A branch of the anterior tibial nerve innervates this muscle.

## MUSCULUS PERONEUS LONGUS

*Form and position:* M. peroneus longus (Pls. 2-8, 16, 20, 26) is a broad, thin, bipennate muscle whose fibers join a broad central tendon. It arises proximally on the extreme tip of the rotular process and on the lateral aspect of the crus by slips which interdigitate with the anterior oblique head of M. flexor perforans et perforatus digiti II, and with the muscular fibers of M. flexor perforans et perforatus digiti III along two-thirds of the length of the crus. On the mesial aspect of the crus the fibers of M. peroneus longus arise from a strong aponeurotic sheet which lies between the internal head of M. gastrocnemius and M. tibialis anticus. This aponeurosis is attached along the entire length of the anteromedial crest of the tibia. About one-fourth of the length of the crus above the intertarsal joint the central tendon and the adjacent anterior oblique fibers turn caudolaterad to lie in the posterior half of the lateral aspect of the distal end of the crus. The tendon then enters the anterolateral part of the tibial cartilage, while a few of its fibers continue on down to attach to the lateral malleolus of the tarsometatarsus.

*Relations:* M. peroneus longus lies superficially on the anterior surface of the crus, between M. flexor perforans et perforatus digiti II posteriorly and the internal head of M. gastrocnemius cranially and mesially. Above the intertarsal joint its tendon lies immediately in front of the tendon of M. flexor perforans et perforatus digiti III.

*Action:* M. peroneus longus accentuates plantar flexion of the tarsus on the crus.

*Nerve supply:* This muscle is innervated by a branch of the anterior tibial nerve.

## MUSCULUS PERONEUS BREVIS

*Form and position:* M. peroneus brevis (Pls. 2-6, 16-20, 25, 26) is a deep muscle that takes its origin from the fibula and the tibiotarsus. The main body of the muscle arises from the fibula and the interosseus membrane and completely enfolds the lower two-thirds of the fibula. It arises from the entire anterior surface of the membrane except for a hiatus through which the peroneal blood vessels pass, and from that part of the

posterior surface of the membrane below the hiatus. Its attachments to the interosseus membrane are such as to allow the peroneal blood vessels to pass through the membrane and between the bones at a point approximately midway down the shaft of the tibia. At the vascular hiatus the distal part of the origin of M. peroneus brevis spreads mesiad over onto the posterolateral surface of the tibiotarsus. Its tibial origin extends distad to about 2.5 cm. above the intertarsal joint. From their origin the fibers of this muscle run distolaterad and enter its heavy tendon on the lateral surface of the lateral condyle of the tibiotarsus. Just above the condyle the tendon is held firmly against the bone by a strong transverse fibrous band. The tendon inserts on the lateral crest of the lateral malleolus of the tarsometatarsus and sends fibers into the lateral strengthening ligament of the tarsal cartilage.

*Relations:* M. peroneus brevis is covered by M. flexor perforans et perforatus digiti III. It is in contact anteriorly with M. tibialis anticus and posteriorly with M. flexor perforatus digiti II. The proximal end of its origin is marked by the bicipital tubercle on the fibula.

*Action:* When the tarsometatarsus is flexed dorsad, M. peroneus brevis aids in extending it (plantar flexion). It also serves as a bracing strut to prevent mesial dislocation of the intertarsal joint.

*Nerve supply:* M. peroneus receives a branch from the anterior tibial nerve.

### MUSCULUS EXTENSOR DIGITORUM LONGUS

*Form and position* (Pls. 6-10, 16, 17, 24, 26): The proximal part of the origin of M. extensor digitorum longus is from the distal two-thirds of the anterior concavity of the rotular process of the tibiotarsus, and from that part of it which lies immediately anterior to the knee-joint. All of its remaining fibers arise from the crista tibiae, slightly below the knee-joint. It is an unipennate muscle with its tendon lying on its lateral aspect next to the tibiotarsus. Just above the distal end of the tibiotarsus the muscle merges completely into a tendon which passes beneath the bony intercondylar bridge of the tibiotarsus. Emerging from the distal end of this bony passage, the tendon runs over the anterior aspect of the intertarsal joint and follows the anterior sulcus of the tarsometatarsus mesial to the double insertion of M. tibialis anticus. Just proximal to the distal end of the tarsometatarsus the tendon divides into its branches for digits II, III and IV.

The two branches for digit II are given off first. These, a medial and a lateral, arise on the mesial side of the tendon, the latter lying on top of and somewhat alongside the former. Just above the metatarsophalangeal joint the lateral tendon to digit II gives off fibers which run laterad to the tendon for digit III. At the proximal end of the first phalanx, the lateral tendon of digiti II splits and inserts, forming a sheath for the underlying medial tendon of digit II. The medial tendon of digiti II then passes on down the digit, broadening as it nears the phalangeal joints and contributing to the fibrous connections of the joints. On the distal end of the second phalanx the tendon spreads distad and inserts all along the third (terminal) phalanx, even to its distal end.

The branches for digits III and IV arise together just below the level of the origin of the two tendons for digit II. The mesial or main tendon for digit III receives the vinculum from the lateral tendon of digit II, and at the same level receives fibers from the ligaments of the metatarsophalangeal joint. From here it passes down the anterior surface of the first phalanx and spreads out over the joint between the first and second phalanges, contributing to the ligaments of the joint. It then continues down on the anteromesial side of the second phalanx, and just distal to the joint between the second and third phalanges it fuses with the lateral tendon of its digit.

The lateral tendon of digit III arises from fibers given off in the angle between the main tendon of digit III and the tendon of digit IV. It also receives fibers which arise from the lateral aspect of the proximal end of the basal phalanx of digit IV and cross superficially the tendon of digit IV. It runs down the first and second phalanges, parallel to the mesial tendon of digit III, contributing fibers to the joint sheath between the second and third phalanges. The lateral and mesial tendons then fuse into a single tendon which extends down the rest of the digit, inserting all along the several bones.

The tendon of digit IV, arising with the two tendons of digit III, extends under the lateral fibers of the lateral tendon of digit II, contributing to the sheaths of the joints between the second and third phalanges, and between the third and fourth phalanges. It then spreads out distally over the fourth and fifth (terminal) phalanges. An accessory tendon of digit IV, arising from the underside of the accessory tendon of digit III, runs parallel to the main tendon of digit IV on the mesial side of the first phalanx, and ends in the joint sheath at the junction of the first and second phalanges.

*Relations:* The origin of M. extensor digitorum longus is enclosed by the medial head of M. tibialis anticus. In the anterior sulcus of the tarsometatarsus its tendon covers the underlying M. extensor brevis digiti IV and M. extensor proprius digiti III.

*Action:* This muscle extends the three anterior digits (II, III and IV), and aids in dorsal flexion of the tarsus on the crus.

*Nerve supply:* M. extensor digitorum longus receives a branch of the anterior tibial nerve.

### MUSCULUS GASTROCNEMIUS

*Form and position:* M. gastrocnemius (Pls. 2-10, 14, 16, 18, 25, 26) has three distinct heads; the external, the medial and the internal. The external head is broad and thick, and arises from the posterior surface of the femur. It extends down the crus, and just above the intertarsal joint it gives rise to the lateral tendon of M. gastrocnemius. At about the level of the superior border of the distal condyles of the tibiotarsus, the lateral tendon unites with the medial tendon, which is formed by both the internal head and the medial head. The internal head arises on the superior part of the mesial aspect of the rotular process of the tibia, from its tip to the knee-joint. Its fibers interdigitate laterally with the fibers of the head of M. peroneus longus and the heavy fascia covering the anterior surface of the knee. This heavy, fleshy, internal head covers the extreme anteromesial border of the crus. Its fleshy fibers unite with those of the medial head and then quickly give rise to the medial tendon, which fuses to the lateral tendon of the external head. The medial head, which covers the internal surface of the tibiotarsus, arises from the femur and from the anteromedial crest of the tibia, just below the knee. Uniting on the posterior surface of the intertarsal joint, the lateral and medial tendons of this muscle form a strong tendon which passes down over the posterior aspect of the intertarsal joint and the tibial cartilage. This tendon is completely enclosed by a fibrous ligament which holds it in place against the posterior surface of the joint. It inserts on the proximal end of the os calcis, which encloses the flexor tendons. Fibers of the gastrocnemius tendon continue down the posterior aspect of the tarsometatarsus to form a sheath which encloses the flexor tendons and binds them into the posterior sulcus.

*Relations:* The external head of M. gastrocnemius is superfiical, being covered only at its cranial end, which lies beneath the caudal portion of M. iliotibialis. M. biceps femoris passes underneath the external head, and the tendinous loop for the support of M. biceps femoris is partially formed by fibers originating on the tendinous mesial aspect of this head. The mesial aspect of the crus is completely covered by the internal head of M. gastrocnemius, and M. plantaris is almost completely enfolded in the lateral and anterior aspects of its medial head.

*Action:* M. gastrocnemius extends the tarsus on the crus.

*Nerve supply:* Branches from the anterior tibial nerve supply this muscle.

### MUSCULUS PLANTARIS

*Form and position:* M. plantaris (Pls. 8-10, 14, 16, 19, 20, 26) arises on the posteromesial surface of the tibiotarsus just below the knee-joint. Its origin is divided into two parts by the proximal end of the insertion of M. popliteus. Only its proximal end is fleshy, from which its slender tendon passes to insert on the mesial side of the superior margin of the tibial cartilage.

*Relations:* M. plantaris is almost completely enclosed by the medial head of M. gastrocnemius.

*Action:* M. plantaris holds in position and elevates the tibial cartilage, and at the same time aids in extending the tarsus.

*Nerve supply:* A branch of the ischiatic nerve supplies this muscle.

### Musculus Flexor Perforatus Digiti II

*Form and position:* M. flexor perforatus digiti II (Pls. 5, 6, 14, 18-21, 25, 26) has two heads, a femoral and an ambiens. The femoral or long head arises from the intercondyloid region of the posterior surface of the femur between the origins of M. flexor perforatus digiti III and M. flexor perforatus digiti IV and that of M. flexor hallucis longus. Halfway down the crus it is joined by fibers of the ambiens head, which arise from the ambiens tendon and its accompanying aponeurosis. The ambiens tendon runs directly into and becomes a part of the substance of this head. The tendon of M. flexor perforatus digiti II enters the proximal end of the tibial cartilage near the middle of the anterior margin of the cartilage. It runs in its own canal through this cartilage, emerging near its anterior side at the middle of its distal margin. The tendon then enters the os calcis and continues down the tarsometatarsus. The tendon of M. flexor perforatus digiti II inserts on the proximal end of the first phalanx of digit II, and a slip from this tendon passes out into the medial web fold.

*Relations:* M. flexor perforatus digiti II is covered externally by M. flexor perforans et perforatus digiti III, and lies between M. peroneus brevis and M. flexor perforatus digiti IV. At the proximal end of the tibial cartilage the tendon of M. flexor perforatus digiti II enters the cartilage in company with the tendons of M. flexor digitorum longus and M. flexor hallucis longus. At this point the tendon of M. flexor perforatus digiti II lies posterior to the tendon of M. flexor digitorum longus and mesial to that of M. flexor hallucis longus, while within the os calcis it lies between these two tendons, and all three are separated from the tendons of the other flexors by a cartilaginous plate. This relationship is maintained to about the middle of the shaft of the tarsometatarsus, where the tendon of M. flexor digitorum longus becomes anterior to the tendon of M. flexor perforatus digiti II. The tendon of M. flexor perforans et perforatus digiti II lies medial to the latter, but at the level of the hallux the tendon of M. flexor perforatus digiti II swings mesiad around to the posterior side of the tendon of M. flexor perforans et perforatus digiti II. At the proximal end of the first phalanx the tendons of M. flexor digitorum longus pars secundus and M. flexor perforans et perforatus digiti II emerge from beneath the tendon of M. flexor perforatus digiti II and pass on down the digit.

*Action:* M. flexor perforatus digiti II flexes the second digit.

*Nerve supply:* A branch from the ischiatic nerve innervates this muscle.

### Musculus Flexor Perforatus Digiti III

*Form and position:* M. flexor perforatus digiti III (Pls. 6-10, 14, 18-20, 25, 26), together with the fleshy fibers of M. flexor perforatus digiti IV, arises from the intercondyloid region of the posterior aspect of the femur just proximal to the origin of M. flexor perforatus digiti II and mesial to the origin of M. gastrocnemius caput externus. M. flexor perforatus digiti III is fleshy only in the lower third of the crus. Its proximal end is an aponeurotic sheet attached to the mesial and anterior sides of M. flexor perforatus digiti IV, and some of its fibers are contributed by the ambiens tendon and its accompanying aponeurosis. Just above the distal end of the tibiotarsus the fleshy fibers of M. flexor perforatus digiti III give rise to a strong rounded tendon which enters a canal on the posterolateral margin of the tibial cartilage. This tendon leaves the tibial cartilage at the lower margin of its midposterior side and passes down the posterior sulcus of the tarsometatarsus. Just above the metatarsophalangeal joint it is connected to the tendon of M. flexor perforans et perforatus digiti III by the vinculum. It then extends over the first (basal) phalanx of digit III, and at the joint between the first and second phalanges of this digit it splits to allow the underlying tendon of M. flexor perforans et perforatus digiti III to emerge. Its insertion is on the lateral and mesial aspects of the basal condyle of the second phalanx.

*Relations:* Just distal and medial to the origin of M. gastrocnemius caput externus on the femur arises a mass of fleshy fibers, on the mesial surface of which is a heavy aponeurosis. The mass of these fibers and their accompanying sheath broaden and thicken considerably as they descend the crus. The aponeurosis divides the fleshy fibers into an anterior and a posterior group. The anterior group forms the main part of M. flexor

perforatus digiti II, and the posterior group forms M. flexor perforatus digiti IV, while the aponeurosis forms the main portion of M. flexor perforatus digiti III. The second head of M. flexor perforatus digiti III arises from the ambiens tendon and aponeurosis, beginning at about the level of emergence of the ambiens tendon from beneath the tendon of M. biceps femoris. This head appears to arise in common with the second head of M. flexor perforatus digiti II. M. flexor perforatus digiti III and M. flexor perforatus digiti IV lie immediately under or mesial to M. gastrocnemius caput externus. At the proximal margin of the tibial cartilage M. flexor perforatus digiti III is in company with the tendons of M. flexor perforans et perforatus digiti III and M. flexor perforatus digiti IV. Within the canal through the cartilage, the tendon of M. flexor perforatus digiti III at first lies mesial to the other two tendons, but it then becomes anterior and finally slightly lateral in position. The lateral position is maintained midway down the tarsometatarsus, where it swings mesiad again to lie medial and superficial to the tendon of M. flexor perforans et perforatus digiti III. Together these two tendons pass over the tendon of M. flexor digitorum longus to digit III. On the first (basal) phalanx the tendon of M. flexor perforatus digiti III, lying superficial to the tendon of M. flexor perforans et perforatus digiti III, forms a sheath over that tendon. At the joint between the first and second phalanges it splits to allow the underlying tendon to emerge.

*Action:* This muscle flexes digit III.

*Nerve supply:* M. flexor perforatus digiti III is innervated by a branch of the ischiatic nerve.

### MUSCULUS FLEXOR PERFORATUS DIGITI IV

*Form and position:* M. flexor perforatus digiti IV (Pls. 2-6, 10, 14, 18-21, 25, 26) arises in the company of M. flexor perforatus digiti III from the intercondyloid region of the posterior aspect of the femur. This muscle, fleshy through most of its course down the crus, gives rise to a rounded tendon which, together with the tendons of M. flexor perforans et perforatus digiti III and M. flexor perforatus digiti III, enters a canal at the posterolateral margin of the tibial cartilage. It leaves the distal end of this cartilage at the middle of its posterior side. The tendon of M. flexor perforatus digiti IV extends down the posterior sulcus of the tarsometatarsus and into digit IV, where it inserts on the sides of the proximal condyle and the shaft of the second phalanx.

*Relations:* M. flexor perforatus digiti IV lies immediately under or mesial to M. gastrocnemius caput externus. Its mesial surface is in close contact with the aponeurotic sheet which gives rise to M. flexor perforatus digiti III. Within the tibial cartilage the tendon of M. flexor perforatus digiti IV lies between those of M. flexor perforans et perforatus digiti III and M. flexor perforatus digiti III. These three tendons together with the tendon of M. flexor perforans et perforatus digiti II form a single bundle to enter the os calcis. Upon leaving the os calcis, the tendon of M. flexor perforatus digiti IV comes from beneath the tendon of M. flexor perforatus digiti III to a lateral position, which it maintains to the distal end of the tarsometatarsus. At the metatarsophalangeal joint the tendon of M. flexor perforatus digiti IV receives on its anterior surface and encloses the tendon of M. flexor digitorum longus pars quartus. Halfway down the first (basal) phalanx it splits to allow the tendon of M. flexor digitorum longus pars quartus to emerge.

*Action:* This muscle flexes digit IV.

*Nerve supply:* A branch of the ischiatic nerve supplies M. flexor perforatus digiti IV.

### MUSCULUS FLEXOR PERFORANS ET PERFORATUS DIGITI II

*Form and position:* M. flexor perforans et perforatus digiti II (Pls. 2-6, 14, 16, 18-21, 25, 26) lies partially superficial on the lateral aspect of the crus between M. gastrocnemius caput externus and M. peroneus longus. In gross appearance the muscle is bipennate and secondarily split into three separate heads which unite into a common tendon at the distal end of the crus. The anterior head is formed by long, fleshy, longitudinal fibers from the lateral surface of the tip of the rotular process, and by short, transverse fibers from the fascia along the middle third of the posterior border of M.

peroneus longus. The medial head consists only of longitudinal fibers from the lateral surface of the rotular process and from the fatty aponeurosis which covers the tip of that process. The posterior head arises from the lateral surface of the external condyle of the femur, the ambiens aponeurosis, and from the crural arm of the biceps loop. These three heads may well be termed the anterior oblique, the median longitudinal, and the posterior oblique heads. The median longitudinal fibers form a broad thin tendon at the level of the knee-joint, and both groups of oblique fibers converge into it in the middle third of the crus. This broad tendon then splits into the three separate tendons, the median of which is very delicate. Just above the intertarsal joint these three tendons reform into a single round tendon, which penetrates the tibial cartilage and the os calcis and runs down the posterior sulcus of the tarsometatarsus. It passes over the first (basal) phalanx of digit II, where it emerges from beneath the overlying tendon of M. flexor perforatus digiti II, and continues on to insert on the lateral and mesial aspects of the basal end of the second phalanx.

*Relations:* The posterior oblique fibers of M. flexor perforans et perforatus digiti II which lies between M. peroneus longus and M. gastrocnemius caput externus, are almost entirely covered by the anterior (lateral) margin of the head of the latter muscle. Just above the intertarsal joint the tendon of M. flexor perforans et perforatus digiti II is directly anterior (lateral) to the lateral tendon of M. gastrocnemius caput externus and posterior (mesial) to that of M. flexor perforans et perforatus digiti III. It enters the posterolateral border of the proximal end of the tibial cartilage and runs obliquely through the canal in the posterior portion of the cartilage to emerge at the posteromesial border of its distal end. Here it joins the tendons of M. flexor perforans et perforatus digiti III, M. flexor perforatus digiti III, and M. flexor perforatus digiti IV. Together these tendons enter the os calcis. Upon leaving this bony tunnel, the tendon of M. flexor perforans et perforatus digiti II lies mesial to that of M. flexor perforans et perforatus digiti III, and posterior to that of M. flexor perforatus digiti II. Halfway down the tarsometatarsus the latter tendon first becomes mesial to that of M. flexor perforans et perforatus digiti II and then swings mesiad around onto the posterior side of that tendon. Thus, at the level of the metatarsophalangeal joint, the tendon of M. flexor perforatus digiti II is posterior and that of M. flexor digitorum longus pars secundus is anterior to the tendon of M. flexor perforans et perforatus digiti II. Along the first phalanx the tendon of M. flexor perforans et perforatus digiti II splits, allowing the tendon of M. flexor digitorum longus pars secundus to cross over the lateral arm and pass between the two arms of the fork. The mesial arm of the fork gives rise to a synovial-like sheath which encloses the tendon of M. flexor digitorum longus pars secundus. The two arms of the fork then reunite over the tendon of M. flexor digitorum longus pars secundus, and finally split again about one centimeter below the union. The lateral fibers of the mesial limb of the first fork remain united to the fibers of the lateral limb, while the remaining fibers of the mesial limb continue down digit II as a sheath. The main (lateral) tendon of M. flexor perforans et perforatus digiti II lies just lateral to the tendon of M. flexor digitorum longus pars secundus. At the joint between the first and second phalanges it splits, the two limbs inserting on the lateral and mesial aspects, respectively, of the proximal end of the second phalanx. The tendon of M. flexor digitorum longus pars secundus passes through this fork from beneath.

*Action:* M. flexor perforans et perforatus digiti II flexes digit II.

*Nerve supply:* It is innervated by a branch from the ischiatic nerve.

### Musculus Flexor Perforans et Perforatus Digiti III

*Form and position:* M. flexor perforans et perforatus digiti III (Pls. 2-6, 14, 16, 18-21, 25, 26) is a fusiform muscle lying on the lateral aspect of the crus, deep to M. flexor perforans et perforatus digiti II and between M. peroneus longus and M. gastrocnemius caput externus. It arises anteriorly along a heavy intermuscular septum lying between it and M. tibialis anticus and M. peroneus longus. At the proximal end of the rotular process some of its fibers arise in common with those of M. flexor perforans et perforatus digiti II. Posteriorly some of its fibers arise from the ambiens aponeurosis and the fascia

covering the crural arm of the biceps loop, some arise from the proximal end of the shaft of the fibula, and others arise from the lateral surface of the external condyle of the femur in company with those of M. flexor perforans et perforatus digiti II. Just above the intertarsal joint the muscle gives rise to a strong round tendon which enters the tibial cartilage at its posterolateral margin and leaves it near the distal margin of its mid-posterior side. The tendon then passes through the os calcis down the posterior sulcus of the tarsometatarsus and crosses onto the posterior surface of the first (basal) phalanx of digiti III to its insertion on the medial and lateral aspects of the basal condyle of the third phalanx.

*Relations:* The proximal half of M. flexor perforans et perforatus digiti III is covered by M. flexor perforans et perforatus digiti II. Just above the tarsal joint its tendon lies between the tendon of M. flexor perforans et perforatus digiti II and that of M. peroneus longus. It enters the tibial cartilage along with the tendon of M. flexor perforatus digiti III and that of M. flexor perforatus digiti IV. Within the cartilage the tendon of M. flexor perforans et perforatus digiti III lies lateral to the other two tendons, but at the point of emergence from the cartilage it passes posterior to the other two tendons and maintains this relationship down to the distal end of the tarsometatarsus, where the tendon of M. flexor perforans et perforatus digiti III becomes lateral and deep to that of M. flexor perforatus digiti III. Slightly above the juncture of the first (basal) and the second phalanges of digit III the tendon of M. flexor perforans et perforatus digiti III emerges through the fork of the tendon of M. flexor perforatus digiti III and becomes superficial again, completely concealing the tendon of M. flexor digitorum longus pars tertius. The latter tendon emerges from beneath the forked tendon of M. flexor perforans et perforatus digiti III at a point just above the juncture of the second and third phalanges.

*Action:* M. flexor perforans et perforatus digiti III flexes digit III.

*Nerve supply:* A branch of the ischiatic nerve supplies this muscle.

## MUSCULUS FLEXOR DIGITORUM LONGUS

*Form and position:* M. flexor digitorum longus (Pls. 4-6, 10, 16, 18-21, 25, 26) is a bipennate deep muscle, lying directly upon the posterior surface of the tibiotarsus and covering the entire posterior aspect of that bone below the knee-joint. Its fibers arise from the posterior margin of the external condyle of the femur, from the posterior surface of the proximal three-fourths of that portion of the tibiotarsus below the knee-joint, and from the head and shaft of all of the posterolateral aspect of the fibula except in the vicinity of the bicipital tubercle, where space is left for the passage of the tendon of M. biceps femoris. Just above the intertarsal joint the muscle forms a slender tendon which enters the proximal end of the tibial cartilage near the middle of its anterior margin. The tendon then passes down the posterior sulcus of the tarsometatarsus, and at a point two-thirds down the length of that bone it gives off a branch to the second digit. Just above the distal end of the tarsometatarsus it gives off another branch to the fourth digit. The remainder of the tendon continues down into the third digit. Each of these tendons inserts broadly on the plantar surface of the terminal phalanx of the digit supplied by it.

*Relations:* Proximally M. flexor digitorum longus covers the fibular end of M. popliteus. The area covered by M. popliteus is the only proximal portion of the posterior aspect of the tibia and fibula from which the fibers of M. flexor digitorum longus do not arise. The distal end of the fleshy part of M. flexor digitorum longus is in contact with M. peroneus brevis. Its tendon penetrates the tibial cartilage in its own separate canal, which lies anterior and slightly mesial to that of the tendon of M. flexor perforatus digiti II. These two tendons, together with the tendon of M. flexor hallucis longus, enter the os calcis, the tendon of M. flexor digitorum longus being the mesial one of the three. About halfway down the tarsometatarsus the tendons of M. flexor hallucis longus and M. flexor digitorum longus fuse. The tendon of M. flexor digitorum longus pars secundus passes over the proximal end of the first (basal) phalanx of the second digit, along with the tendon of M. flexor perforans et perforatus digiti II. Just

beyond this point the former tendon spirals over the lateral limb of the latter to enter its fork and become deep as the limbs of the fork of M. flexor perforans et perforatus digiti II reunite. A sheath is formed over this section of the tendon by fibers which arise from the mesial limb and attach to the lateral limb of the forking tendon of M. flexor perforans et perforatus digiti II. At the second fork of this tendon, the tendon of M. flexor digitorum longus pars secundus emerges and becomes superficial, although it is still covered by a thin sheath of fibers from the former tendon. The tendon of M. flexor digitorum longus pars secundus inserts broadly on the plantar surface of the distal half of the third (terminal) phalanx of digit II.

The tendon of M. flexor digitorum longus pars tertius is covered by the tendons of M. flexor perforatus digiti III and M. flexor perforans et perforatus digiti III. Just above the joint between the second and third phalanges it becomes superficial by emerging between the limbs of the latter tendon. Held in place against the third phalanx by circular and longitudinal fibers continuing down from the tendon of M. flexor perforans et perforatus digiti III, it inserts on the fourth (terminal) phalanx of digit III.

The tendon of M. flexor digitorum longus pars quartus is enclosed by the tendon of M. flexor perforatus digiti IV. It emerges on the first (basal) phalanx from between the limbs of the latter and continues down to insert on the fifth (terminal) phalanx of digit IV.

*Action:* M. flexor digitorum longus flexes the three anterior digits (II, III and IV).

*Nerve supply:* Innervation for this muscle is supplied by a branch from the ischiatic nerve.

### MUSCULUS FLEXOR HALLUCIS LONGUS

*Form and position:* M. flexor hallucis longus (Pls. 5, 6, 14, 16, 20, 21, 26) arises from the posterior surface of the external condyle of the femur. It is a small muscle whose size and shape are comparable to that of M. plantaris. Its short fleshy portion gives rise to a long thin tendon which extends down the posterior aspect of the shaft of the tibia and enters the tibial cartilage near the middle of its anterior margin. Upon leaving the tibial cartilage the tendon passes through the os calcis and continues down the posterior sulcus of the tarsometatarsus. About halfway down the tarsometatarsus it fuses with the tendon of M. flexor digitorum longus. It does not send a branch to the hallux (first digit).

*Relations:* At its origin the lateral surface of M. flexor hallucis longus is covered by the ambiens aponeurosis. Its anterior surface is in contact with the proximal end of M. flexor digitorum longus and M. popliteus, while its mesial surface lies against M. gastrocnemius caput medius. Its tendon lies in its own separate canal within the tibial cartilage, but upon entering and leaving the cartilage it lies immediately lateral to the tendons of M. flexor perforatus digiti II and M. flexor digitorum longus.

*Action:* M. flexor hallucis longus assists M. flexor digitorum longus in flexing the anterior digits (II, III and IV).

*Nerve supply:* The ischiatic nerve furnishes a branch for this muscle.

### MUSCULUS POPLITEUS

*Form and position:* M. popliteus (Pls. 10, 16, 26) is a broad and heavy but short muscle whose fibers run across the leg on the posterior aspect of the neck of the tibia and of the fibula. Its fibular end is attached by fibers along a vertical line on the lateral surface of the head, neck, and shaft of the fibula. The fleshy fibers run almost at right angles to the tibia and the fibula and pass over the posterior surface of both to attach to the posteromesial surface of the tibia immediately below the knee-joint.

*Relations:* The tibial end of M. popliteus lies just posterior to the origin of M. plantaris, and is partially covered by the belly of that muscle. The remainder of M. popliteus is in contact posteriorly with M. flexor digitorum longus and M. flexor hallucis longus.

*Action:* M. popliteus is a medial rotator of the crus.

*Nerve supply:* This muscle is innervated by a branch from the ischiatic nerve.

### MUSCULUS ABDUCTOR DIGITI II

*Form and position:* M. abductor digiti II (Pls. 17, 22, 26) is a very small muscle arising on the mesial aspect of the distal end of the tarsometatarsus and its medial condyle. Its proximal tip is immediately below the distal end of the point of attachment of the free metatarsal I to the tarsometatarsus. Its tendon crosses the metatarsophalangeal joint to insert on the medial surface of the proximal end of the first (basal) phalanx of the second digit.

*Relations:* M. abductor digiti II is covered only by the skin and fascia of the tarsus and toes. It lies mesial to but not in contact with the tendon of M. extensor digitorum longus.

*Action:* This muscle abducts the second digit.

*Nerve supply:* A branch of the anterior tibial nerve supplies M. abductor digiti II.

### MUSCULUS ABDUCTOR DIGITI IV

*Form and position:* M. abductor digiti IV (Pls. 18-21, 23, 25, 26) arises along the distal half of the lateral edge of the posterior sulcus of the tarsometatarsus and along the distal portion of the floor of that sulcus just above the intermetatarsal foramen. It is a unipenniform muscle whose tendon lies along the lateral ridge of the posterior sulcus, passes down over the lateral surface of the condyle for the fourth digit, and inserts on the lateral side of the proximal end of the first (basal) phalanx of the fourth digit.

*Relations:* M. abductor digiti IV lies lateral to M. adductor digiti IV. Although it is in direct contact with the underlying bone, because of its extreme lateral position it is not covered by any of the tendons of the flexor muscles.

*Action:* This muscle is an abductor of digit IV.

*Nerve supply:* No nerve branch for this muscle was found, but it probably receives its supply from the anterior tibial nerve.

### MUSCULUS ADDUCTOR DIGITI II

*Form and position:* M. adductor digiti II (Pls. 20, 21, 23, 25, 26) lies in the posterior sulcus of the tarsometatarsus. It arises from the proximal half of that bone, beginning just below the os calcis. It is almost completely tendinous, its narrow tendon running down along the medial ridge of the sulcus and passing over the lateral surface of the condyle for the second digit to insert on the lateral surface of the proximal end of the first (basal) phalanx of digit II.

*Relations:* M. adductor digiti II lies directly upon the floor of the posterior sulcus of the tarsometatarsus and is entirely covered by the overlying tendons of the flexor muscles which run down this sulcus.

*Action:* This muscle adducts digit II.

*Nerve supply:* Although no nerve was found leading into this muscle, it probably receives innervation by way of the anterior tibial nerve.

### MUSCULUS ADDUCTOR DIGITI IV

*Form and position:* M. adductor digiti IV (Pls. 21, 23, 25, 26) lies along the lateral margin of the posterior sulcus of the tarsometatarsus. It arises from the distal portion of the floor and the lateral ridge of this sulcus. Its tendon inserts on the postero-medial surface of the proximal end of the first (basal) phalanx of digit IV.

*Relations:* This muscle is deep to the tendons of the flexor muscles which pass down the posterior sulcus of the tarsometatarsus. It lies medial to M. abductor digiti IV and lateral to M. adductor digiti II.

*Action:* M. adductor digiti IV adducts the fourth digit.

*Nerve supply:* A branch from the anterior tibial nerve innervates this muscle.

### Musculus Extensor Proprius Digiti III

*Form and position:* M. extensor proprius digiti III (Pls. 23, 24, 26) is a very small muscle arising on the anterior aspect of the distal end of the tarsometatarsus from a depression between the condyles for digits III and IV. It extends across the metatarsophalangeal joint and inserts on the anterolateral surface of the proximal end of the first (basal) phalanx of digit III.

*Relations:* M. extensor proprius digiti III lies beneath the tendon of M. extensor digitorum longus for digit III, and just medial and slightly anterior to the tendon of M. extensor brevis digiti IV.

*Action:* This muscle extends digit III slightly. It has its greatest value as an antagonist to the flexors.

*Nerve supply:* The anterior tibial nerve supplies this muscle.

### Musculus Extensor Brevis Digiti IV

*Form and position:* M. extensor brevis digiti IV (Pls. 23, 24, 26) is a bipennate muscle which lies in the anterior sulcus of the tarsometatarsus. It is almost entirely of tendon, fleshy fibers being found only along its line of origin. It arises from the bone all along its course, which begins at the proximal end of the tarsometatarsus just lateral to the insertion of M. tibialis anticus, and forms a tendon which, running next to the bone, enters a foramen just above the distal condyles and emerges deep between the condyles for digits III and IV to insert on the anteromesial aspect of the proximal end of the first (basal) phalanx of digit IV.

*Relations:* At its proximal end M. extensor brevis digiti IV lies lateral to the insertion of M. tibialis anticus. It and its tendon are covered anteriorly by the tendon of M. extensor digitorum longus. As the tendon emerges from the bone between the condyles for digits III and IV, it lies lateral and deep to M. extensor proprius digiti III.

*Action:* This muscle extends digit IV, but, like M. extensor proprius digiti III, its major role is as an antagonist to the flexors.

*Nerve supply:* A branch of the anterior tibial nerve innervates this muscle.

### Musculus Extensor Hallucis

*Form and position:* M. extensor hallucis (Pls. 18-22, 25, 26) is a very small muscle confined to the area of the hallux and its supporting metatarsal. It arises by three or four slips from the proximal end of the posterior (concave) surface of metatarsal I. Its fleshy fibers form a thin, slender tendon which extends across the metatarsophalangeal joint to insert on the posteromesial side of the first (basal) phalanx of digit I.

*Relations:* M. extensor hallucis is isolated from all other muscles, due to the fact that only this and M. flexor hallucis brevis supply the hallux.

*Action:* This muscle extends or flexes digit I dorsad.

*Nerve supply:* It receives a branch from the anterior tibial nerve.

### Musculus Flexor Hallucis Brevis

*Form and position:* M. flexor hallucis brevis (Pls. 18-22, 25, 26) is almost entirely tendinous. It arises by very short fibers from the distal end of the posteromedial surface of the tarsometatarsal aponeurosis, lies along the lateral side of the hallux, and inserts on the anterolateral surface of the first (basal) phalanx of digit I.

*Relations:* Nowhere is this muscle in contact with or in close proximity to any other muscle. It lies mesial to the flexor tendons which pass down the posterior sulcus of the tarsometatarsus.

*Action:* This muscle produces slight plantar flexion of digit I. It also adducts digit and metatarsal I towards the midline.

*Nerve supply:* No branch was found entering M. flexor hallucis brevis, but it probably receives innervation from the anterior tibial nerve.

TABLE 1.—Attachments of muscles

| | Vert. Column | Ilium | Ischium | Pubis | Femur | Tibio-tarsus | Fibula | Tarso-metatar. | Metatarsal I | Phalanges | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Abductor digiti II | | | | | | | | o | | x | |
| Abductor digiti IV | | | | | | | | o | | x | |
| Adductor digiti II | | | | | | | | o | | x | |
| Adductor digiti IV | | | | | | | | o | | x | |
| Add. long. et brev. | | | o | o | x | | | | | | |
| Ambiens | | | | o | | | | | | | 1 |
| Biceps femoris | o | o | | | | | x | | | | |
| Ext. brev. d. IV | | | | | | | | o | | x | |
| Extensor dig. long. | | | | | | o | | | | x | |
| Extensor hallucis | | | | | | | | | o | x | |
| Ext. pro. dig. III | | | | | | | | o | | x | |
| Fem.-tib. externus | | | | | o | x | | | | | |
| Fem.-tib. internus | | | | | o | x | | | | | |
| Fem.-tib. medius | | | | | o | x | | | | | |
| Flexor dig. long. | | | | | | o | o | | | x | |
| Flexor hall. brev. | | | | | | | | | | x | 2 |
| Flexor hall. long. | | | | | o | | o | | | | 3 |
| Fl. p. et p. d. II | | | | | o | o | | | | x | |
| Fl. p. et p. d. III | | | | | o | o | | | | x | |
| Fl. p. d. II | | | | | o | | | | | x | |
| Fl. p. d. III | | | | | o | | | | | x | |
| Fl. p. d. IV | | | | | o | | | | | x | |
| Gastr. externus | | | | | o | | | x | | | |
| Gastr. internus | | | | | | o | | x | | | |
| Gastr. medius | | | | | o | | | x | | | |
| Glut. med. et min. | | o | | | x | | | | | | |
| Iliacus | | o | | | x | | | | | | |
| Ilio-tibialis | o | o | | | | x | | | | | |
| Ilio-troch. ant. | | o | | | x | | | | | | |
| Ilio-troch. med. | | o | | | x | | | | | | |
| Ilio-troch. post. | o | o | | | x | | | | | | |
| Ischio-femoralis | | o | o | | x | | | | | | |
| Obtur. externus | | | o | o | x | | | | | | |
| Obtur. internus | | | o | o | x | | | | | | |
| Peroneus brevis | | | | | | o | o | x | | | |
| Peroneus longus | | | | | | o | | | | | 4 |
| Pirif. caud.-fem. | o | | | | x | | | | | | |
| Pirif. ilio-fem. | | o | | | x | | | | | | |
| Plantaris | | | | | o | o | | | | | 4 |
| Popliteus | | | | | | x | o | | | | |
| Sartorius | o | o | | | | x | | | | | |
| Semimembranosus | | | o | | | x | | | | | |
| Semitendinosus | | o | | | | x | | | | | |
| Tibialis anticus | | | | | o | o | | x | | | |

1 Inserts into heads of flexors of digits. 2 Arises from an aponeurotic sheet. 3 Tendon fuses with that of M. fl. d. longus. 4 Ends in tibial cartilage. o—origin, x—insertion.

TABLE 2.—Functions of muscles

| | Hip-joint | | | | | | Knee-joint | | | | Tarsal-joint | | Digital-joints | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Ext. | Flex. | Abd. | Add. | L. Rot. | M. Rot. | Ext. | Flex. | L. Rot. | M. Rot. | Plant. Fl. | Dors. Fl. | Ext. | Flex. | Abd. | Add. |
| Abductor digiti II | | | | | | | | | | | | | | | x | |
| Abductor digiti IV | | | | | | | | | | | | | | | x | |
| Adductor digiti II | | | | | | | | | | | | | | | | x |
| Adductor digiti IV | | | | | | | | | | | | | | | | x |
| Add. long. et brev. | | x | | | x | | | | | | | | | | | |
| Ambiens | | | | | | x | x | | | | | | | | | |
| Biceps femoris | | x | | | | x | | | x | | | | | | | |
| Ext. brev. d. IV | | | | | | | | | | | | | x | | | |
| Extensor dig. long. | | | | | | | | | | | | x | x | | | |
| Extensor hallucis | | | | | | | | | | | | | x | | | |
| Ext. pro. dig. III | | | | | | | | | | | | | x | | | |
| Fem.-tib. externus | | | | | | | | | x | | | | | | | |
| Fem.-tib. internus | | | | | | | | | | x | | | | | | |
| Fem.-tib. medius | | | | | | | x | | | | | | | | | |
| Flexor dig. long. | | | | | | | | | | | x | | | x | | |
| Flexor hall. brev. | | | | | | | | | | | | | | x | | |
| Flexor hall. long. | | | | | | | | | | | x | | | | | |
| Fl. p. et p. d. II | | | | | | | | | | | x | | | x | | |
| Fl. p. et p. d. III | | | | | | | | | | | x | | | x | | |
| Fl. p. d. II | | | | | | | | | | | x | | | x | | |
| Fl. p. d. III | | | | | | | | | | | x | | | x | | |
| Fl. p. d. IV | | | | | | | | | | | x | | | x | | |
| Gastr. externus | | | | | | | | x | | | x | | | | | |
| Gastr. internus | | | | | | | | x | | | x | | | | | |
| Gastr. medius | | | | | | | | x | | | x | | | | | |
| Glut. med et min. | | | x | | | | | | | | | | | | | |
| Iliacus | | | | x | x | | | | | | | | | | | |
| Ilio-tibialis | | | x | | | | | | x | | | | | | | |
| Ilio-troch. ant. | x | | | | | x | | | | | | | | | | |
| Ilio-troch. med. | x | | | | | x | | | | | | | | | | |
| Ilio-troch. post. | x | | | | | x | | | | | | | | | | |
| Ischio-femoralis | | x | | | | | | | | | | | | | | |
| Obtur. externus | | x | | | x | | | | | | | | | | | |
| Obtur. internus | | x | | | x | | | | | | | | | | | |
| Peroneus brevis | | | | | | | | | | | x | | | | | |
| Peroneus longus | | | | | | | | | | | x | | | | | |
| Pirif. caud.-fem. | | x | | | x | | | | | | | | | | | |
| Pirif. ilio-fem. | | x | | | x | | | | | | | | | | | |
| Plantaris | | | | | | | | | | | x | | | | | |
| Popliteus | | | | | | | | | | x | | | | | | |
| Sartorius | x | | | | | | x | | | x | | | | | | |
| Semimembranosus | | x | | | | | | x | | x | | | | | | |
| Semitendinosus | | x | | | | | | x | | x | | | | | | |
| Tibialis anticus | | | | | | | | | | | | x | | | | |

## Discussion

### ACTION OF THE LEGS IN SWIMMING AND DIVING

C. W. Townsend (1909) reported many observations which indicate that in diving the loon presses its wings closely against the side of its body and propels itself through the water by leg action alone. He also cited reports which tend to show that under some conditions the wings are raised slightly and sometimes are used vigorously. These observations imply that the wings are used to aid in attaining a sudden burst of speed and for balancing while turning.

According to Townsend's observations, in swimming and diving the loon thrusts its legs caudad simultaneously in a series of strokes. Townsend's observations are borne out by the observations of Professor Perry W. Gilbert of Cornell University, who placed a loon in a swimming tank and took motion pictures of its swimming and diving strokes. On the basis of these pictures he reported (oral citation) that the loon uses its feet simultaneously.

Its narrow pelvis and short femur, and its long crus and tarsus enable the bird to bring the plantar surfaces of the feet near one another behind the body. The tibia is further elongated by the rotular process, which projects far anterior to the knee-joint, thus providing the length of skeleton necessary to carry the long fibers on which the extensor muscles of the digits depend for their strength and range of contraction.

From my own observations on non-captive loons, from descriptions of Dabelow (1925) and of Frank and Neu (1929), and from inference drawn from the structure of the body, I believe that the description given in the paragraph below presents a reasonably accurate picture of the action of the legs of the loon under water.

At the beginning of the stroke the tarsus is flexed forward so that its posterior margin faces outward and its anterior aspect lies folded against the anterior (lateral) surface of the crus, which is fixed parallel to the axis of the bird. The toes lie bent in a ventrolateral direction, and are close together with the web closed. The tarsus is swung first laterad and then backward, with the plantar surface of the foot directed caudad, and simultaneously the toes are abducted and the web is spread. At the end of the stroke the tarsus is fully extended on the crus, forming with it a straight line, and the feet lie converged behind the body. The entire movement of the tarsus and foot is along a nearly horizontal plane. Recovery to the starting position is accomplished by dorsal flexion of the tarsus, adduction of the toes, and plantar flexion of the digits towards the tarsus. Because of its sharp anterior margin and strong lateral compression the tarsus offers little resistance to the water while moving forward to the starting position.

Dabelow (1925) describes the action of the feet of the loon as being like that used by a seal and as being advantageous in that this convergent movement of the feet shoves a greater mass of water behind the body than would be transposed by a nonconvergent or parallel type of movement (such as is used by the cormorant). He further states that this great mass of water forced through a relatively small opening (the space between the tips of the

converging feet and the ventral surface of the trunk and tail) against the relatively stationary mass of water behind it will actually propel the body of the bird forward (with somewhat of a jet action).

## Analysis of the Functions of the Muscles

In attaining the starting position for the stroke, forward flexure of the tarsus is accomplished by the tibialis anticus, assisted to some extent by the extensor digitorum longus, which lies deep to the former muscle. The femur remains immovable at the hip-joint, and the tibiotarsus is similarly fixed at the knee-joint by the contour of its bony articulations and by the powerful muscles of the hip and thigh which act as antagonists to each other.

Sixteen muscles fix the hip-joint. Ten of these arise on some part of the pelvic girdle, the vertebral column, or both, and insert on the femur. These ten muscles are the iliotrochantericus anticus, the iliotrochantericus medius, the iliotrochantericus posticus, the gluteus medius et minimus, the iliacus, the obturator externus, the obturator internus, the adductor longus et brevis, the piriformis, and the ischiofemoralis. Primitively the three iliotrochanterici are extensors of the hip-joint, while the ischiofemoralis, the adductor longus et brevis, and the piriformis are flexors, antagonistic to these three muscles. The gluteus medius et minimus is an abductor, and the iliacus, its antagonist, is an adductor. The obturator externus and the obturator internus are lateral rotators, assisted by the iliacus, the adductor longus et brevis, and the piriformis. Antagonistic to these five muscles are two medial rotators—the iliotrochanterici, of the extensor group, and the biceps femoris, which originates on the vertebral column and inserts on the fibula.

The other six muscles which help to fix the hip-joint extend beyond the femur and insert on the tibiotarsus, and serve as fixators of both the knee-joint and the hip-joint. These muscles are the sartorius, the iliotibialis, the semitendinosus, the semimembranosus, the ambiens, and the biceps femoris. The sartorius is an extensor of the hip-joint as well as of the knee-joint, while the biceps femoris, the semitendinosus, and the semimembranosus are flexors of both joints. The iliotibialis is an abductor of the thigh and a lateral rotator of the crus, while the ambiens, although without a bony insertion, is an adductor of the thigh and to some extent an extensor of the crus.

In addition to the sixteen muscles listed above which act on the hip- and knee-joints, another muscle, the femoritibialis, assists in fixing the knee-joint. This muscle arises from the femur, inserts on the tibiotarsus, and acts on the crus alone. It consists of three parts—the internus, the medius, and the externus. In primitive amniotes and in most birds this muscle gives rise to a tendon which inserts on the proximal face of the patella. In the loon, however, the medius and the internus are fleshy throughout, and only the externus and a few fibers of the medius attach to the patellar tendon. The internus inserts on the mesial aspect of the head of the tibia immediately anterior to the tibial notch, approximating its position of insertion in the majority of the birds, but the medial part of the femoritibialis inserts on the entire posterior aspect of the rotular process, which represents an elongation of the anterior tibial protuberance of other tetrapods, including most birds. This elongated

rotular process is associated wtih the immobilization of the knee joint. Extension, the primary function of the femoritibialis, having been succeeded by fixation in the loon, its area of insertion in this bird is wide and its tail is fleshy after the form of a typical fixator.

Extension is not a possible action for either the femoritibialis internus or the femoritibialis externus in the loon, since their insertions are not on that area of the head of the tibia in front of the joint as they are in most amniotes, but are on the mesial and lateral aspects of the joint at the base of the rotular process. The function of these two parts in this animal is primarily that of rotation of the crus on the femur.

The femoritibialis in the loon is an excellent example of a change of insertion which results in a change of action. Modifications of muscles are for the most part in size and shape, and in their extent of origin, which is usually widely spread over the bony surface. These modifications may decrease or increase the power and effectiveness of a muscle, but a change in position of the insertion, which usually occupies a point or a narrow line where the force of the muscle is concentrated, usually cannot vary greatly without altering the action of the muscle.

From the starting position of the stroke in swimming, the tarsus of the loon is swung laterad and caudad by action of the gastrocnemius. This powerful three-headed muscle is assisted by the peroneus longus and the peroneus brevis. The gastrocnemius arises partly from the femur and partly from the head of the tibia. Its internal head arises on the internal aspect of the rotular process, in the same relative position that it occupies on the anterior tibial protuberance in most other birds. This relationship supports the theory that the rotular process is an elongation of the anterior tibial protuberance. With the elongation of the protuberance, the area for the origin of this head of the gastrocnemius has been enlarged.

Dabelow (1925) points out that the gastrocnemius is the most important extensor of the tarsometatarsus and that the situation of this muscle gives it three advantages for modification in the loon. First, being elevated more or less out of the mass of other muscles of the crus which surrounds it, its developmental possibilities are only slightly limited. Second, the elongation of this muscle makes possible a greater arc of movement for the tarsometatarsus. Third, the origin of the gastrocnemius usually is on the posterior margin of the tibia below the knee-joint, and so in the extended foot, the line joining its origin with its tendinous insertion lies parallel to the long axis of the tarsometatarsus, which it extends. However, when the origin of the gastrocnemius moves forward, as it has in the loon, so that it lies on the tip of the cranially-projecting rotular process, the proximal end of the muscular axis lies in front of the tarsometatarsal axis and the distal end behind it. By this displacement of the muscle it produces complete extension of the joint with relatively little contraction.

The seven primitively flexor muscles which pass over the posterior aspect of the intertarsal joint and flex the toes also play a minor role in the extension of the tarsus on the crus. Though their primary action is plantar flexion of the toes, during the backward movement of the feet they contract and do

not flex but rather aid in preventing hyperextension of the toes under pressure against the water. By their position they assist the gastrocnemius in extending the tarsus. These flexors pass through the tibial cartilage, which is held taut in its position on the posterior aspect of the intertarsal joint and during extension of the tarsus is elevated by the rather small plantaris and peroneus longus muscles.

As the tarsus moves caudad, the toes are spread by action of the extensor digitorum longus, assisted by the short extensor proprius digiti II, extensor brevis digiti IV, and abductors digiti II and IV. The extensor digitorum longus has a broad origin from almost the entire anterior aspect of the rotular process of the tibiotarsus and the proximal end of the shaft of that bone. The arrangement of its tendons on the digits is such that by its contraction the toes are abducted and the web is spread with its plantar surface facing caudad. As the tarsus continues to move caudad, the iliotibialis and the femoritibialis externus rotate the crus slightly laterad and dorsad so that the feet are converged behind the body. At the end of the backward stroke the digits of opposite feet are touching one another, and the whole of the extremity below the femur is almost in a straight line.

As the foot begins its recovery movement craniad, the flexors of the toes and the adductors of digits II and IV fold the toes and web. The tibialis anticus is the primary dorsal flexor of the tarsus. This very powerful muscle arises over a great extent of the anterior aspect of the tibiotarsus, including the rotular process. Corresponding to the primitive nature of its function, the structure and position of this muscle show little modification from the generalized condition, other than increase in length. At the beginning of the dorsiflexion the tibialis anticus is assisted by the extensor digitorum longus, which lies underneath it. As soon as the tarsus begins to flex dorsally the latter muscle no longer aids but hinders the action of the tibialis anticus; it then relaxes and the toes relax and dangle from the distal end of the tarsometatarsus. The tibialis anticus, aided by the internal rotators—femoritibialis internus, sartorius, semitendinosus, and semimembranosus—of the crus, completes the movement of the tarsus to its starting position.

## MUSCLE-TENDON RELATIONSHIPS IN FIXATION

Most of the sixteen muscles which serve as fixators or functional ligaments of the hip- and knee-joints are fleshy throughout. This structure correlates with the fact that powerful muscles with little movement may serve this function. According to Grant (1940), fleshy fibers of a muscle contract by one-third to one-half of their resting length. Thus the distance through which the site of insertion may move is one-third to one-half of the length of the fleshy part of the muscle. Fixators, functioning not so much in moving a joint as in immobilizing it, may be short and fleshy. It is possible that contractile fibers are retained by fixator muscles because of their elasticity rather than being transformed into noncontractile fibers which would fix the joint but would not absorb shock, even though the animal has had sufficient time in which to evolve reduction to tendon. Those muscles which are not fleshy throughout—the piriformis, the semitendinosus, and the semimembrano-

sus—but which give rise to an inserting tendon, are long muscles whose points of attachment are far removed from each other.

Maintenance of fleshy fibers, which have a high metabolic rate and relatively large volume, is expensive to the economy of an animal. Tendons, however, being composed of relatively inert tissue and occupying relatively little space, are inexpensive. Correlatively, fleshy fibers are rarely longer than necessary to accomplish the amount of contraction required, their tendons providing the additional length needed. If the distance between origin and insertion is greater than the length of the fleshy fibers required for full action, the span may be completed by either tendon or aponeurosis. Certain muscles —the biceps femoris, the obturator internus, the ambiens, and the iliotibialis— pass through supporting bony, ligamentous or tendinous structures, or across joints where wear may occur. Tendons or aponeuroses also occur in the pertinent regions of these muscles to resist wear.

## THE PATELLA

The tendinous distal end of the femoritibialis pars externus, and the inserting tendon of the iliotibialis together form the patellar tendon. This common tendon in the loon encloses a small, free flake of bone (though in immature birds it is mainly cartilage, often with a mere trace of ossification in the center) which is the patella.

The patella of birds and mammals is typically a sesamoid bone on the anterior aspect of the knee-joint in the tendon of the major extensor muscles of the crus. This region in the loon is entirely occupied by the elongate rotular process of the tibia. Wagner (1843:121) and Owen (1866:83) described the loon as lacking a free patella, and claimed that it had been fused with this rotular process. Shufeldt (1884:328) stated that the patella of the loon ". . . is reduced to a diminutive flake of bone, articulating above the base [of the rotular process of the tibia] on its posterior aspect." D'Arcy Thompson (1890) objected to Shufeldt's interpretation and claimed that ". . . the patella proper of the Divers [loons] has fused with the cnemial crest [of the tibia], and that the small patelliform plate [of Shufeldt] is to be regarded as a **sesamoid* and not a homologue of the free patella found in *Podiceps, Hesperornis* and other forms."

Coues (1866:159) regarded a ". . . very small process of bone" on the superior border of the tibio-femoral joint ". . . as the true analogue of the patella." Later (1903:1048) he describes the patella as ". . . rudimentary." Lucas (1909:18), in Knowlton's *Birds of the World,* said: ". . . In Grebes and Loons the upper end of the tibia is greatly extended and the knee-pan [patella] is correspondingly reduced, appearing as a small splint of bone back of the process." The structure of the process in the grebes is quite different from that in the loons. The patella of the grebe is a large, distinct, pyramidal bone on the entire posterior aspect of the rotular process, while the patella of the loon as described by Shufeldt is merely a ". . . small splint." Pycraft (1910:384), in his *A History of Birds*, agrees with Shufeldt, stating that

* The italics are those of the present author.

". . . the patella or knee-cap is represented in the loons only by a vestige in the shape of a small flake of bone." In the same work (p. 452) he says ". . . the cnemial processes of the grebe are enormously developed, . . ., and are overtopped by the great pyramidal patella, which in the Divers the loons has become suppressed by the great cnemial crest."

Heilman (1926:50) says that in ". . . *Colymbus*" (the loon) the patella ". . . forms a considerable projection from the proximal end in the longitudinal axis of the bone [tibiotarsus]."

I believe that the small flake of bone, described by Shufeldt and Pycraft, is a true patella which has been suppressed, as Pycraft suggested, in correlation to the enormous elongation of the anterior tibial protuberance. This flake of bone is discernible on dissection of adult specimens, and in one excellently prepared skeleton of *Gavia immer* in the Chicago Natural History Museum (No. 105378), the patella was preserved in situ. In this specimen it may be seen as a true flake of bone held in place by ligaments (patellar ligament) from the base of the rotular process. On neither the right nor the left knee does the patella show any connection with the fibula. On the left knee only a very few fibers run to it from the front of that part of the femur below it, and on the right knee a single band of fibers running from the femur above, passes transversely into the top of the patella. Both of these femoral connections probably are the persisting fibers of the femoritibialis externus. The patella of the loon occupies approximately the same area on the knee as does the lower lateral margin of the much larger patella of the grebe. It is probable that the patella of the loon has undergone suppression upward from the rotular process until only a bare trace of it remains.

## Summary

A description of the forty-one muscles of the pelvic appendage in the loon, *Gavia immer,* and an analysis of the function of these muscles during swimming are given in this paper.

Twenty-five specimens of the Common Loon (*Gavia immer*) were used in the study. The specimens were fixed in 10% formalin and preserved in an embalming solution, and studied through gross dissection with the aid of low power lenses.

The terminology used in this paper is based upon that used by Hudson (1937). A table of synonymy showing the terminology used by seven investigators of avian anatomy is presented.

The loon is totally unable to walk about on land after the manner of most birds. Terrestrial movement is limited to a sliding along the ground on the breast, the bird pushing itself along by kicking backward with both feet simultaneously, as in swimming.

In swimming the feet are moved simultaneously in a series of backward strokes. The entire stroke takes place along a nearly horizontal plane with the tips of the toes of opposite feet converging to touch one another at the end of the stroke.

Of the forty-three pelvic muscles present in birds, the loon possesses forty-

one. The two not present are M. extensor brevis digiti III, described by Gadow (1891) for the Ratitae, and M. lumbricalis, described by Hudson (1937) for the Green Heron. Hudson pointed out that "this muscle is often very small and rudimentary, hence it is difficult to determine whether is is absent or simply vestigial." However, there was no tissue in the foot of the loon that could be taken for a vestigial M. lumbricalis. The only short extensor for digit III is the M. extensor proprius digiti III. There is no femoral insertion nor accessorium semitendinosi for M. semitendinosus.

The bony attachments of the pelvic muscles are presented in a table.

The functions of the pelvic muscles are summarized in tabular form.

The hip- and knee-joints are almost immovably fixed in position by sixteen muscles. Movement at these joints is confined to rotation.

The intertarsal joint is the first joint of the appendage to be entirely free from the body wall and is situated at the level of the base of the tail. At this joint the tarsus is hinged and swings freely along a nearly horizontal plane.

The fixators of the hip- and knee-joints are for the most part well developed and fleshy. The retention of fleshy fibers in certain of these fixators is possibly related to the need for elastic structures which may absorb the shock of strains placed upon them. Tendons or aponeuroses in other fixators possibly have developed in relation to the great distances to be spanned between origin and insertion, to reduce the size and weight of the spanning structures, or to resist wear at points where these members cross joints or pass through guiding structures.

The anterior tibial protuberance has been elongated craniad in the loon to form the rotular process.

The patella does not take part in the formation of the rotular process, but is a free flake of bone in the common tendon of M. iliotibialis and M. femoritibialis externus.

Possession of nearly all of the muscles found in birds indicates that the loon has in this respect a primitive type of muscular system. However, many of its muscles and the skeletal parts supporting them show marked modifications in form and function, in correlation with the specialized method by which it progresses in water.

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## ABBREVIATIONS IN PLATES

(Stippled areas indicate origins of muscles, diagonal lines indicate insertions of muscles)

I—Digit I
II—Digit II
III—Digit III
IV—Digit IV

Abd. d. II—M. abductor digiti II
Abd. d. IV—M. abductor digiti IV
Acet.—Acetabulum
Add. brev.—M. adductor brevis
Add. d. II—M. adductor digiti II
Add. d. IV—M. adductor digiti IV
Add. long.—M. adductor longus
Add. long. et brev.—M. adductor longus et brevis
Amb.—M. ambiens
Amb. gr.—Ambiens groove
Ant. cocc. n.—Anterior coccygeal nerve
Ant. lat.—Antero-lateral crest
Ant. med.—Antero-medial crest
Ant. tib. n.—Anterior tibial nerve

Ant. troc.—Anti-trochanter
Art. n.—Articular notch

Bic.—Bicipital tubercle
Bic. fem.—M. Biceps femoris
Bic. loop—Biecps loop

Cap.—Capitulum
Cond. lat.—Lateral condyle
Cond. med.—Medial condyle
Crur. n.—Crural nerve
Depr. cocc.—M. depressor coccygeus

Ext. brev. d. IV—M. extensor brevis digiti IV
Ext. dig. l.—M. extensor digitorum longus
Ext. hal.—M. extensor hallucis
Ext. pro. d. III—M. extensor proprius digiti III

Fem.—Femur
Fem. tib.—M. femori-tibialis
Fem. tib. ext.—M. femori-tibialis externus
Fem. tib. int.—M. femori-tibialis internus
Fem. tib. med.—M. femori-tibialis medius
Fib.—Fibula
Fl. dig. l.—M. flexor digitorum longus
Fl. hal. l.—M. flexor hallucis longus
Fl. hal. brev.—M. flexor hallucis brevis
Fl. p. d. II—M. flexor perforatus digiti II
Fl. p. d. III—M. flexor perforatus digiti III
Fl. p. d. IV—M. flexor perforatus digiti IV
Fl. p. et p. d. II—M. flexor perforans et perforatus digiti II
Fl. p. et p. d. III—M. flexor perforans et perforatus digiti III
For. isch.—Foramen ischiaticus
For. obt.—Foramen obturator

Gastr.—M. gastrocnemius
Gastr. ext.—M. gastrocnemius caput externus
Gastr. int.—M. gastrocnemius caput internus
Gastr. med.—M. gastrocnemius caput medius
Glut. med. et min.—M. gluteus medius et minimus

Il.—Ilium
Iliacus
Il. cocc.—M. ilio-coccygeus
Il. pub.—M. ilio-pubis
Il. sp.—Ilias spine
Il. tib.—M. ilio-tibialis
Il. troc.—M. ilio-trochanterici
Il. troc. ant.—M. ilio-trochantericus anticus
Il. troc. med.—M. ilio-trochantericus medius
Il. troc. post.—M. ilio-trochantericus posticus
Isch.—Ischium
Isch. fem.—M. ischio-femoralis
Isch. n.—Ischiatic nerve

Lev. cocc.—M. levator coccygeus
Lig.—Ligament within os calcis
Lig. ant.—Anterior ligament
Lig. lat.—Lateral ligament
Lig. per.—Peroneal ligament

Met. I—Metatarsal I
Met. II—Metatarsal II
Met. III—Metatarsal III
Met. IV—Metatarsal IV

Obt. ext.—M. obturator externus
Obt. int.—M. obturator internus
Obt. n.—Obturator nerve
Os calcis

P. rot.—rotular process
Per. brev.—M. peroneus brevis
Per. long.—M. peroneus longus
Phal.—Phalanges
Pirif.—M. piriformis
Pirif. p. caud. fem.—M. piriformis pars caudo-femoralis
Pirif. p. il. fem.—M. piriformis pars ilio-femoralis
Plant.—M. plantaris
Popl.—M. popliteus
Ps.—Pygostyle
Pub.—Pubis
Pub. pr.—pubic process
Pub. sp.—pubic spine

Sart.—M. sartorius
Semim.—M. semimembronosus
Semisp.—M. semispinalis dorsi
Semit.—M. semitendinosus
Sp. neur.—Neural spine of free dorsal vertebrae
Ss.—Synsacrum

Tar.-met.—Tarso-metatarsus
Tib.—Tibio-tarsus
Tib. ant.—M. tibialis anticus
Tib. cart.—Tibial cartilage
Tr. pr.—Transverse process of free dorsal vertebrae
Troc.—Trochanter

Urop. gl—Uropygial gland

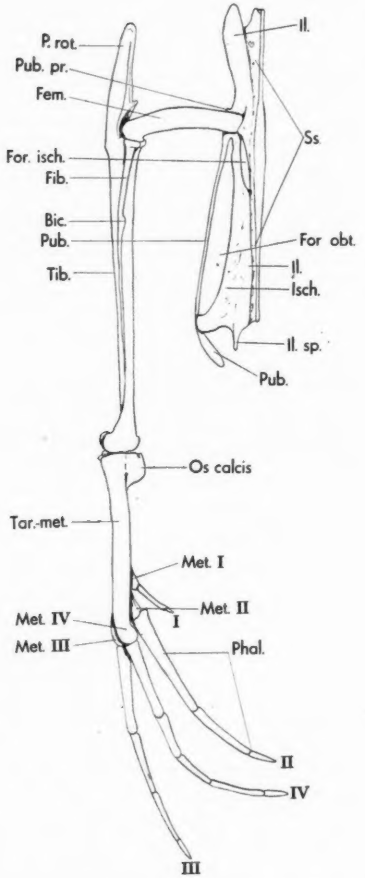


Plate 1.—Dorsal view of the bones of the left half of the pelvis and synsacrum, and of the left leg ×1/3

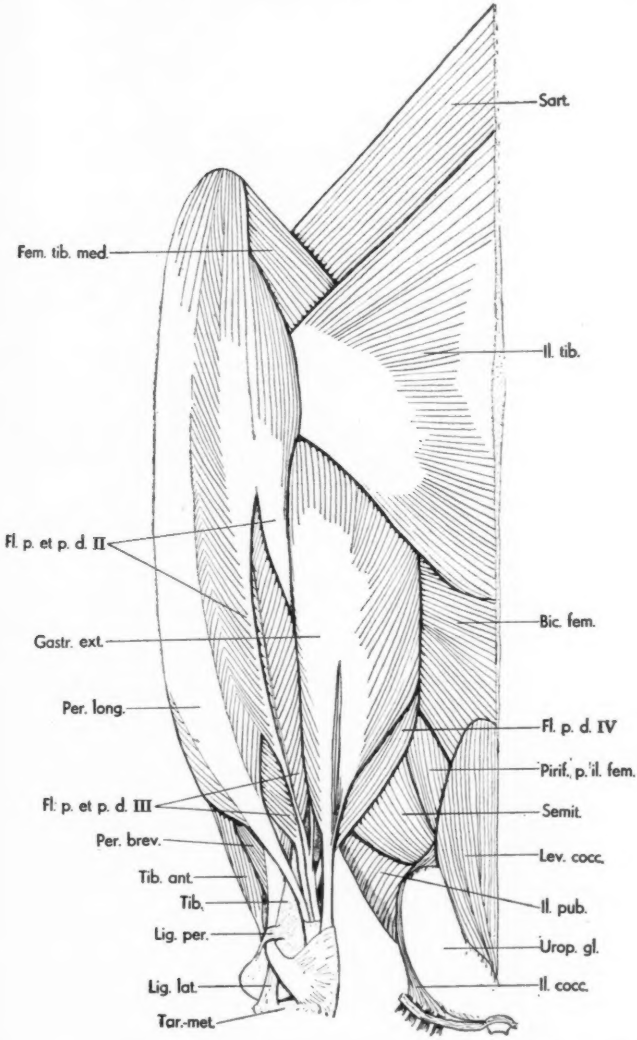


Plate 2.—Dorsal view of left hip, thigh and crus after removal of the skin ×2/3

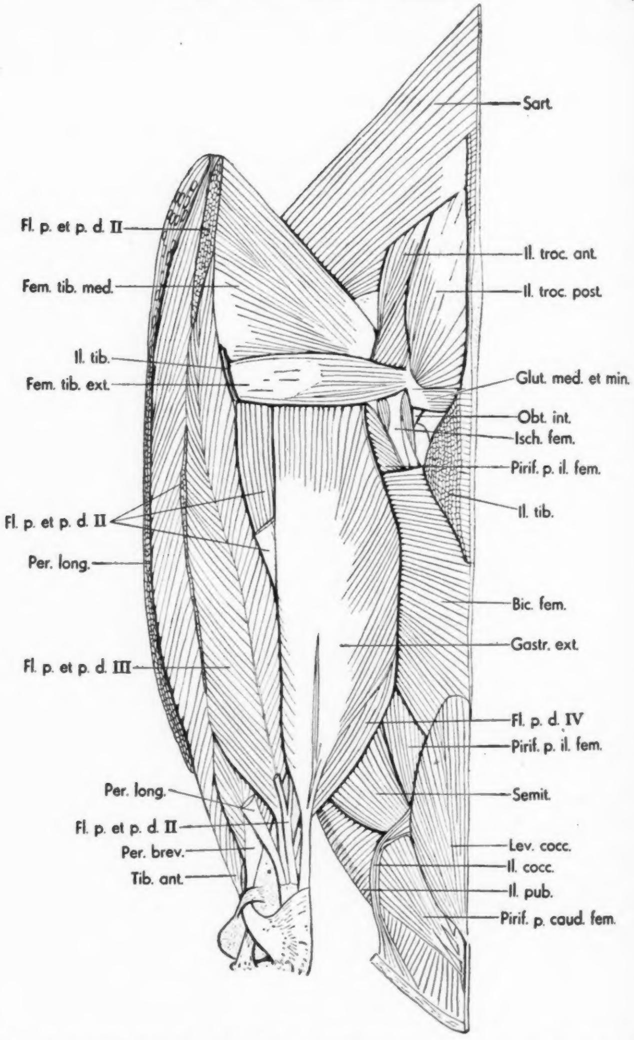


Plate 3.—Dorsal view of left hip, thigh and crus after partial removal of *M. iliotibialis, M. peroneus longus, M. flexor perforans et perforatus digiti II, M. ilio-coccygeus,* and *M. piriformis pars caudo-femoralis* ×2/3.

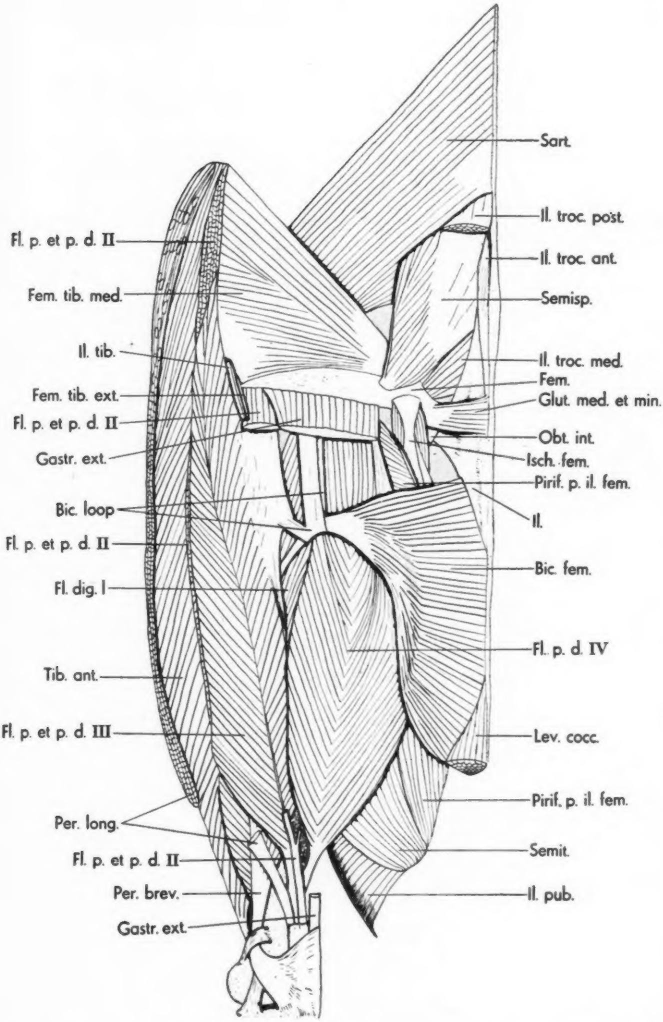


Plate 4.—Dorsal view of left hip, thigh and crus, after partial removal of *M. iliotrochantericus posticus* and *M. gastrocnemius caput externus*, in addition to those listed as removed for Plate 3, ×2/3.

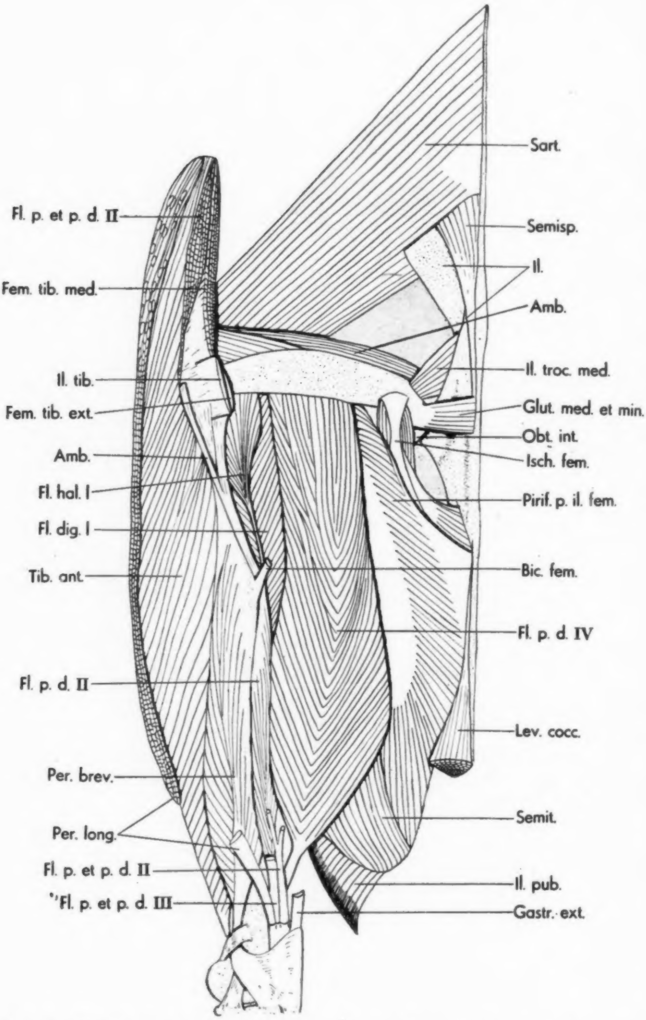


Plate 5.—Dorsal view of left hip, thigh and crus after partial or complete removal of *M. ilio-trochantericus anticus, M. biceps femoris, M. femoritibialis medius,* and *M. flexor perforans et perforatus digiti III,* in addition to those listed as removed for plates 3 and 4, ×2/3.

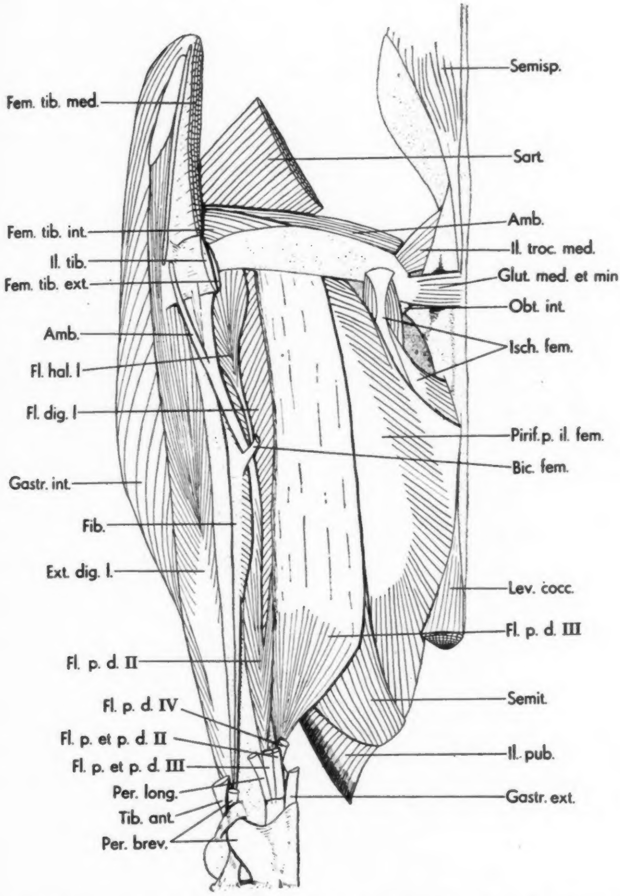


Plate 6.—Dorsal view of left hip, thigh and crus after partial or complete removal of *M. sartorius, M. flexor perforatus digiti IV, M. tibialis anticus, M. peroneus brevis,* in addition to those listed as removed for plates 3, 4 and 5, ×2/3.

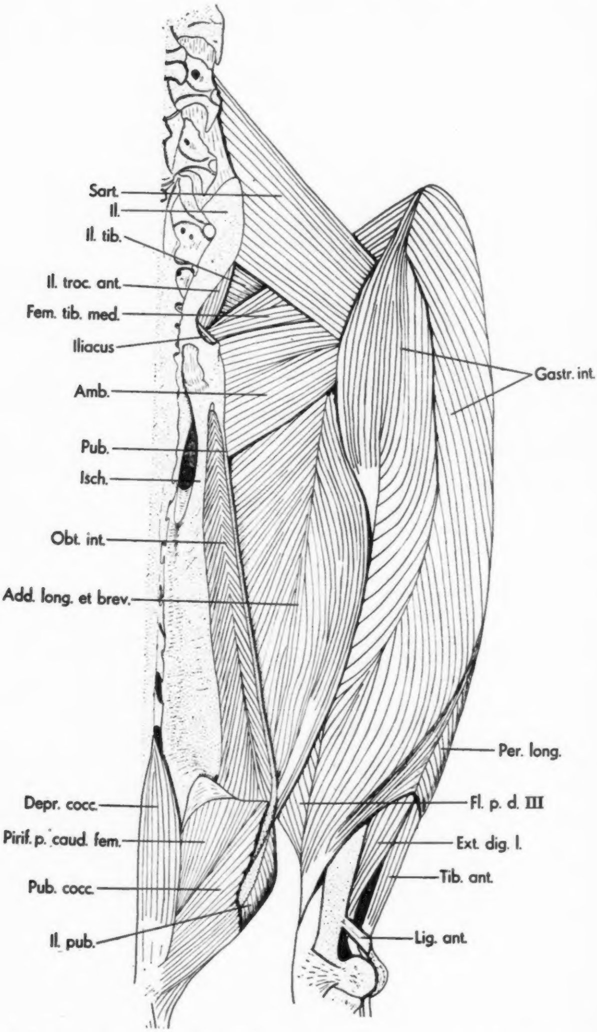


Plate 7.—Ventral view of left hip, thigh and crus after removal of the skin ×2/3

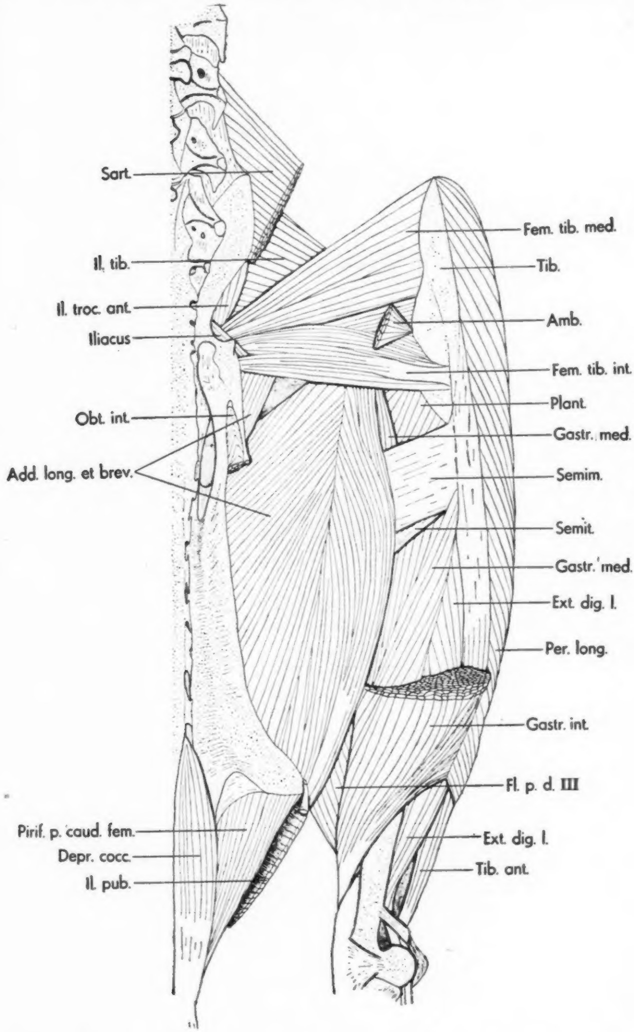


Plate 8.—Ventral view of left hip, thigh and crus, after partial or complete removal of *M. sartorius*, *M. ambiens*, *M. gastrocnemius caput internus*, *M. ilio-pubis*, *M. pubococcygeus*, *M. obturator internus*, and the pubis ×2/3.

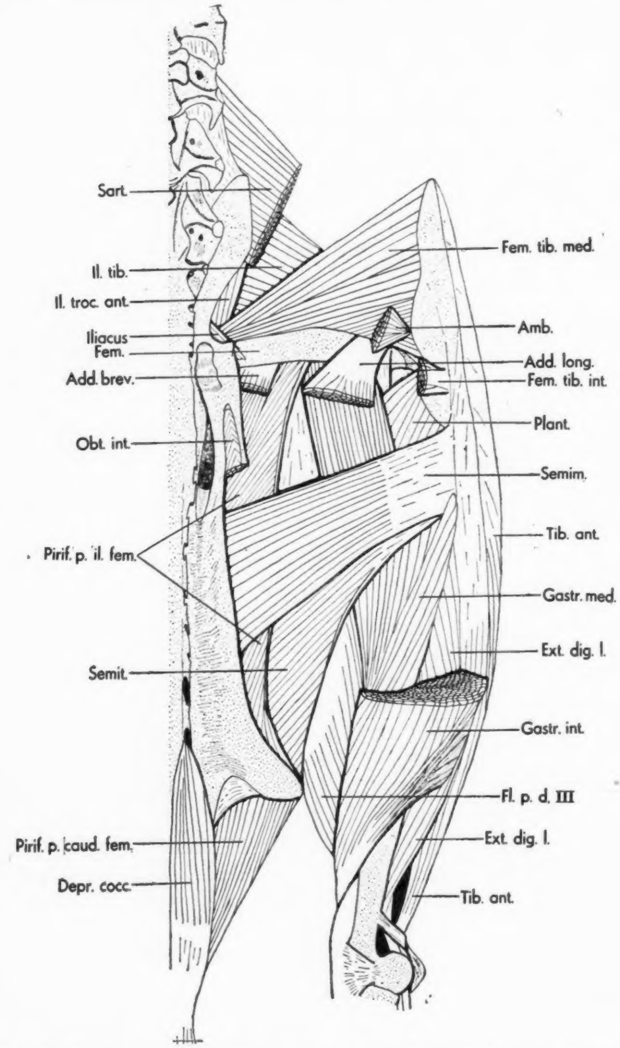


Plate 9.—Ventral view of left hip, thigh and crus after partial or complete removal of *M. femori-tibialis internus*, and *M. adductor longus et brevis*, in addition to those listed as removed for plate 8, ×2/3.

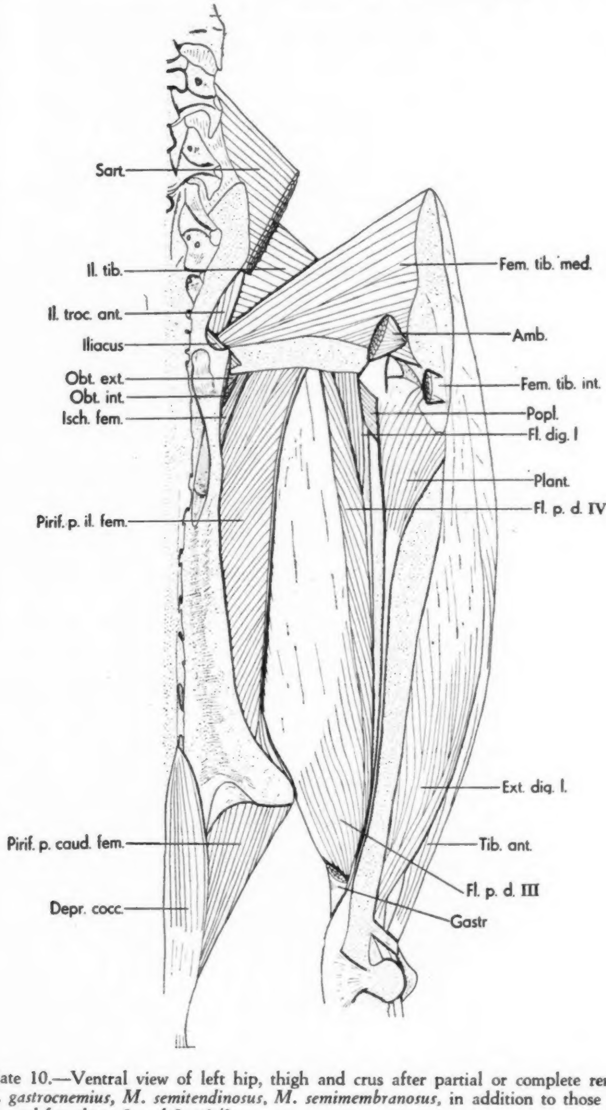


Plate 10.—Ventral view of left hip, thigh and crus after partial or complete removal of *M. gastrocnemius, M. semitendinosus, M. semimembranosus,* in addition to those listed as removed for plates 8 and 9, ×2/3.

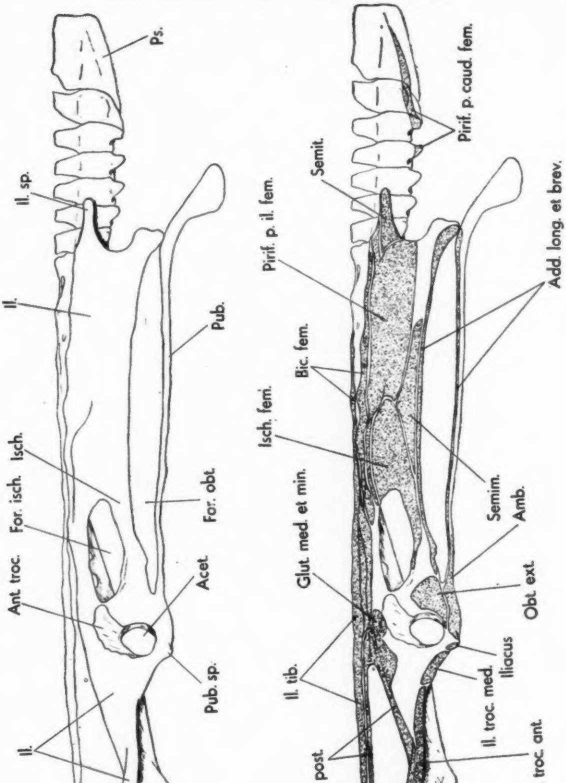


Plate 11. Figs. 1, 2.—1. Lateral view of left pelvis with adjacent parts of vertebral column (left); 2. Lateral view of left pelvis with adajacent parts of vertebral column, showing muscular attachments (right) ×2/3.

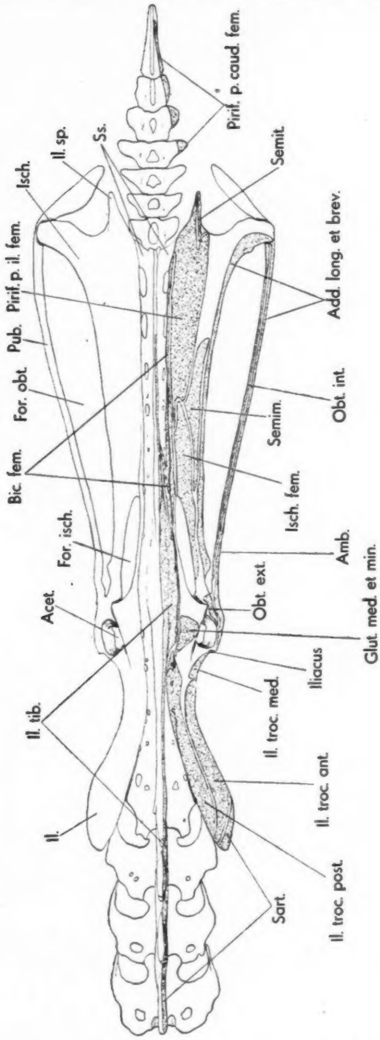


Plate 12.—Dorsal view of pelvic girdle, synsacrum and adjacent regions of vertebral column, showing muscular attachments on the left side ×2/3

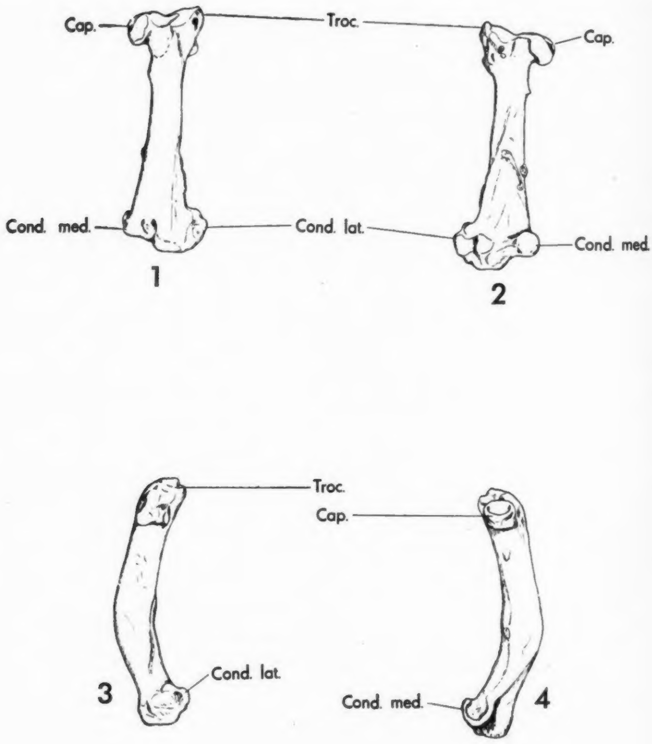


Plate 13. Figs. 1-4. Left femur ×2/3.—1. Anterior aspect; 2. Posterior aspect; 3. Lateral aspect; 4. Mesial aspect

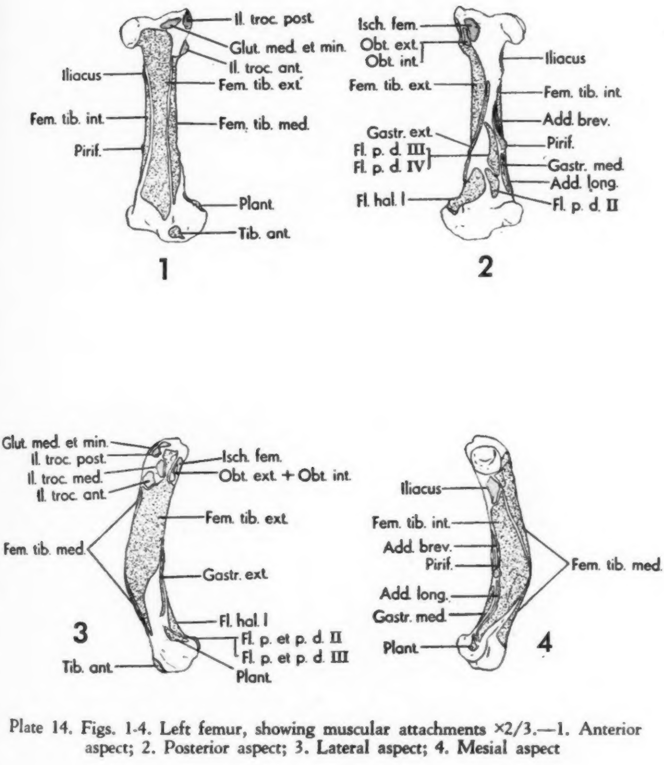


Plate 14. Figs. 1-4. Left femur, showing muscular attachments ×2/3.—1. Anterior aspect; 2. Posterior aspect; 3. Lateral aspect; 4. Mesial aspect

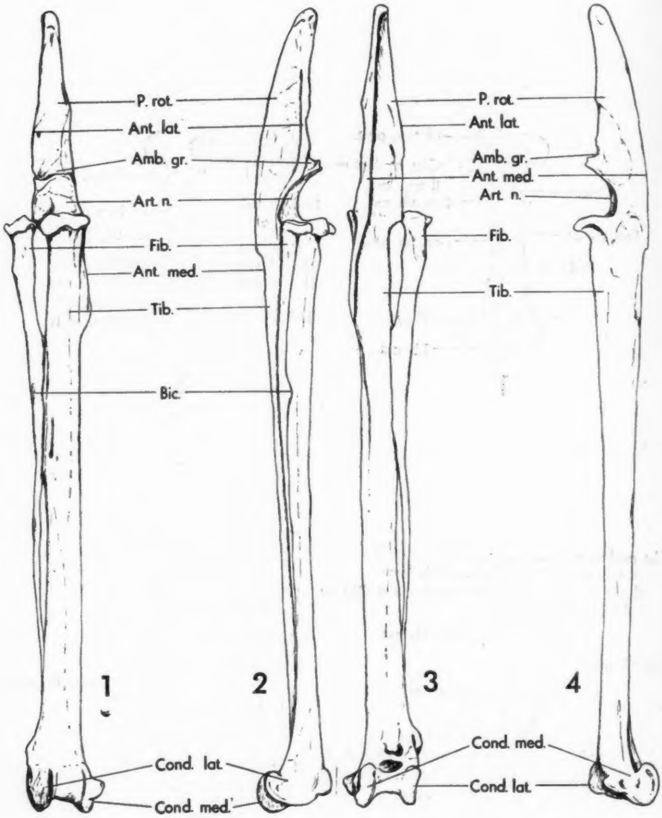


Plate 15. Figs. 1-4. Bones of the left crus ×2/3.—1. Posterior aspect; 2. Lateral aspect; 3. Anterior aspect; 4. Mesial aspect

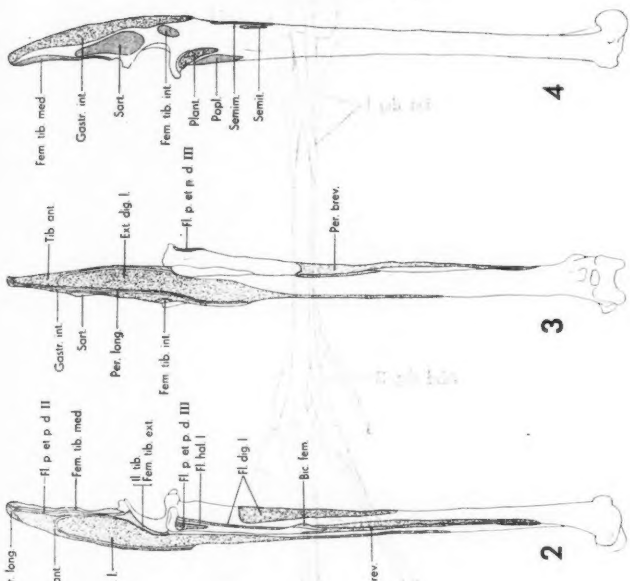


Plate 16. Figs. 1-4. Bones of the left crus, showing muscular attachments ×2/3. —1. Posterior aspect; 2. Lateral aspect; 3. Anterior aspect; 4. Mesial aspect

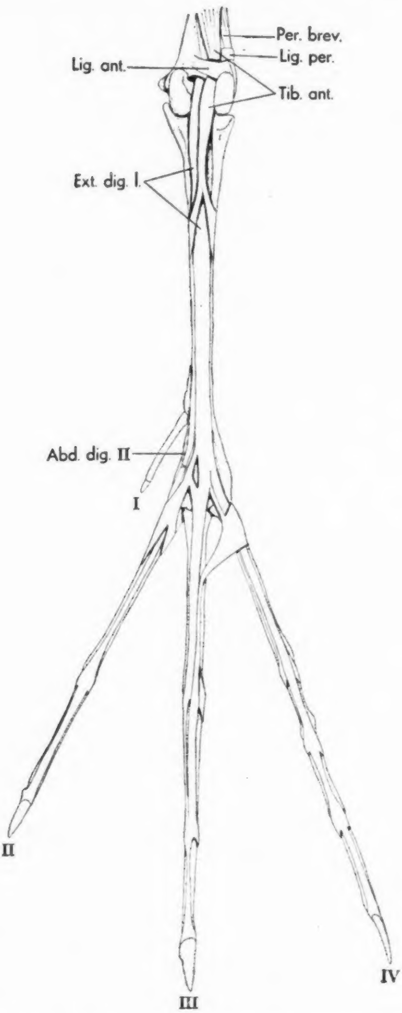


Plate 17.—Anterior or extensor side of left foot after removal of the skin ×2/3

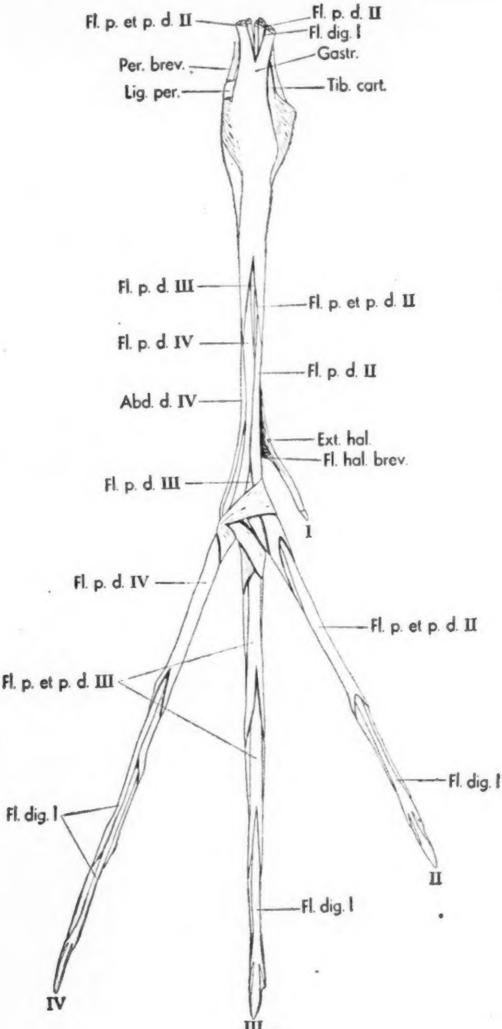


Plate 18.—Posterior or flexor side of left foot after removal of the skin ×2/3

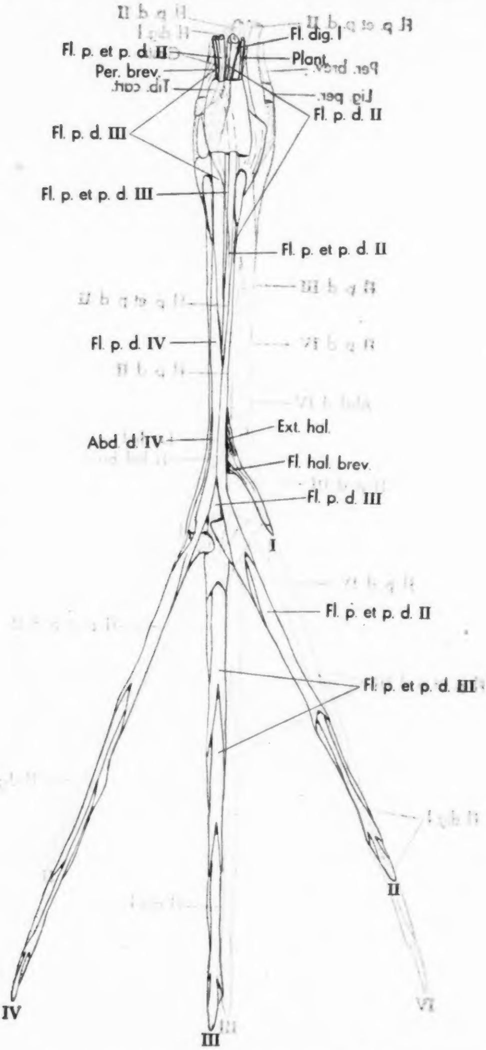


Plate 19.—Posterior or flexor side of left foot after removal of *M. gastrocnemius* and its binding ligaments. Os calcis is partially cut away ×2/3

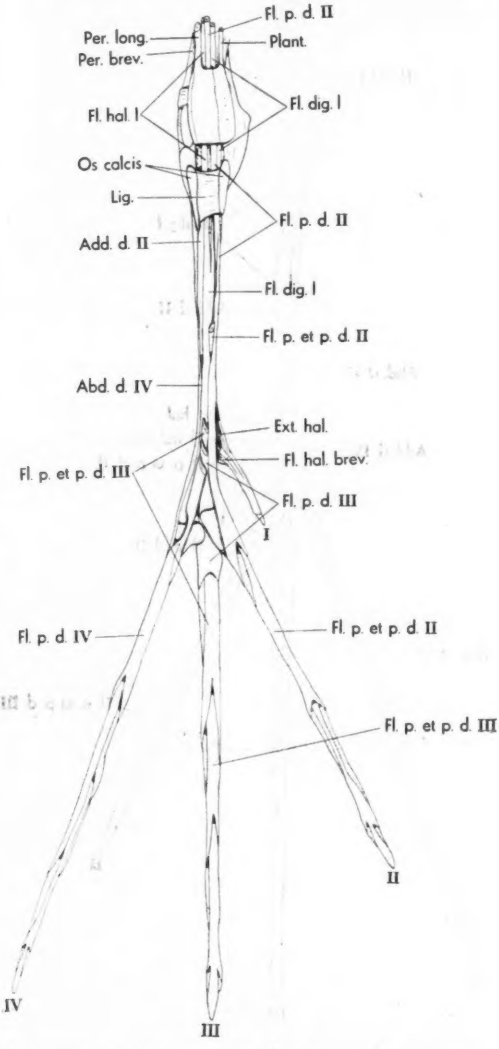


Plate 20.—Posterior or flexor side of left foot after partial or complete removal of *M. flexor perforatus digiti III*, *M. flexor perforatus digiti IV*, *M. flexor perforans et perforatus digiti II*, *M. flexor perforans et perforatus digiti III*, in addition to those listed as removed for plate 19, ×2/3.

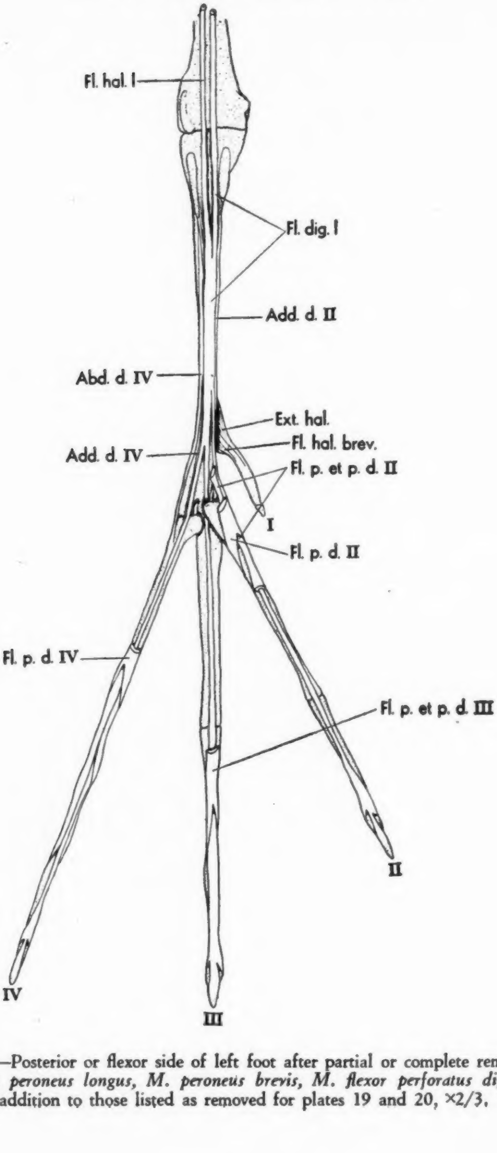


Plate 21.—Posterior or flexor side of left foot after partial or complete removal of *M. plantaris, M. peroneus longus, M. peroneus brevis, M. flexor perforatus digiti II,* and ligaments, in addition to those listed as removed for plates 19 and 20, ×2/3.

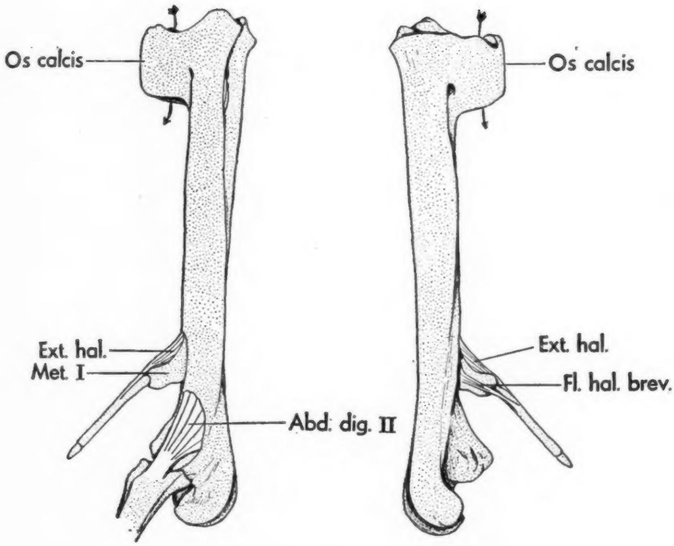


Plate 22. Deep musculature of left tarso-metatarsus ×1.—1. Mesial aspect (left); 2. Lateral aspect (right). Arrow through tunnel of os calcis

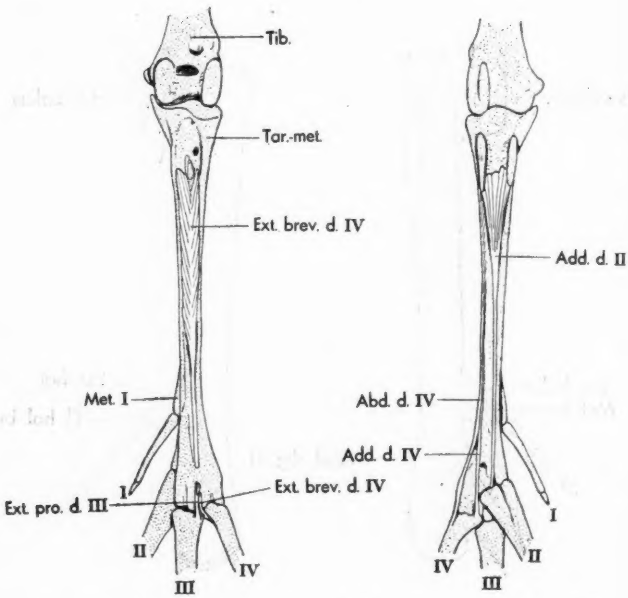


Plate 23. Deep musculature of left tarso-metatarsus ×2/3.—1. Anterior or extensor aspect (left); 2. Posterior or flexor aspect (right)

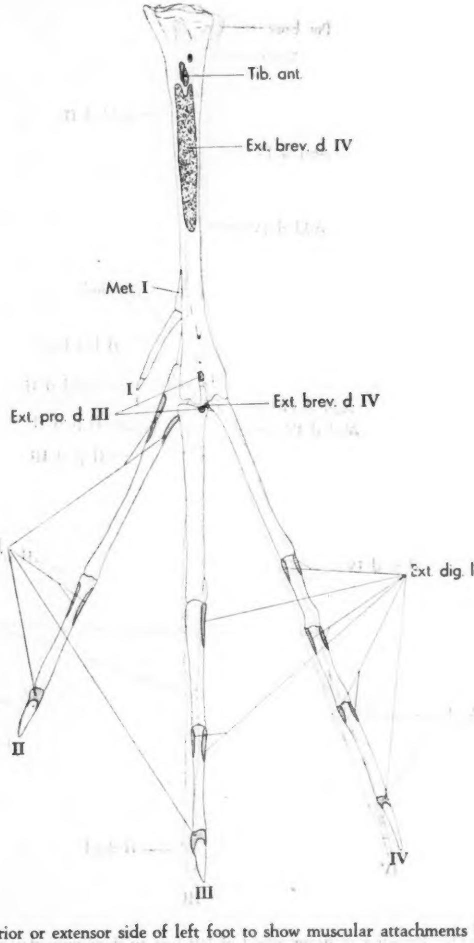


Plate 24.—Anterior or extensor side of left foot to show muscular attachments ×2/3

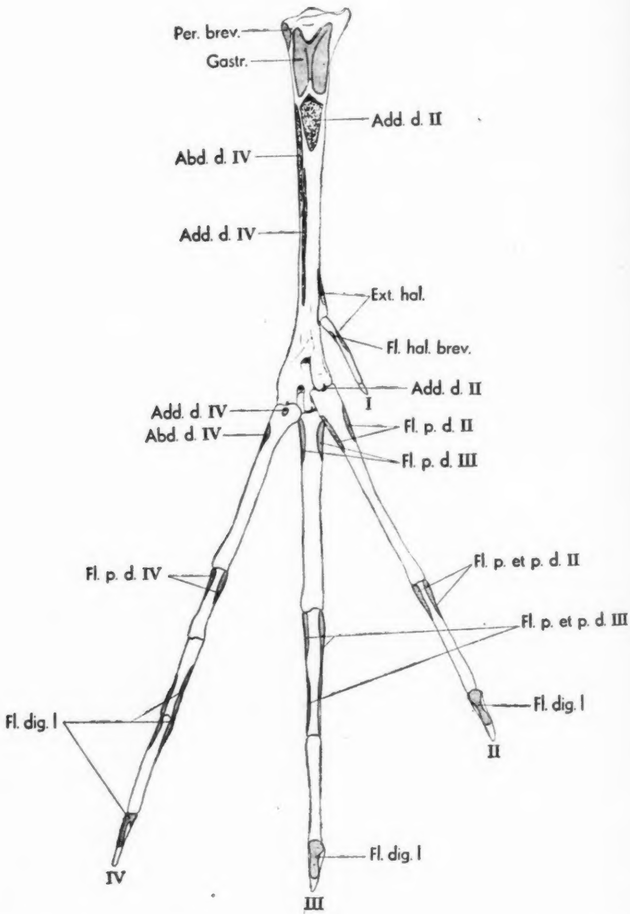


Plate 25.—Posterior or flexor aspect of left foot to show muscular attachments ×2/3

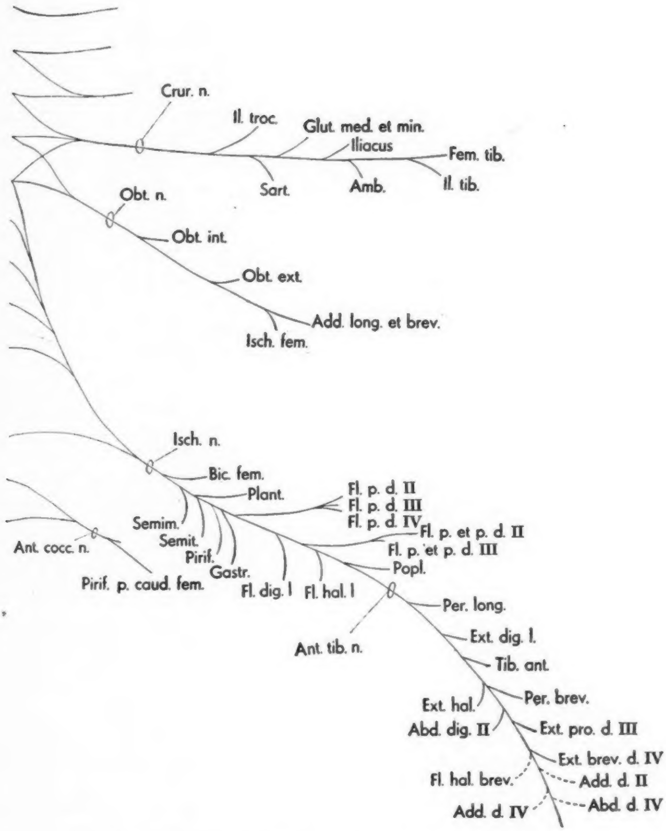


Plate 26.—Schematic diagram of innervation of pelvic musculature

# List of the Snakes of the United States and Canada by States and Provinces

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*Cornell University, Ithaca, N. Y.*

State and provincial lists of the species of snakes of the United States and Canada are here brought together, more particularly for the use of the layman and the young tyro who may want to know his state ophidian fauna. It is hoped that it may be of some help to the expert, if only for quick reference. Each state has two lists, one of the accredited forms (in the sense of accepted, certain, verified); and one of the problematic ones (in the senses of hypothetical, accidental, introduced, puzzling, questionable, unverified, or extinct). We realize that these lists invite criticism, but if students are stimulated, we shall be satisfied.

We do not need to discuss at length the accredited list. Sometimes under "problematic" we put the scientific name now approved and sometimes the form used at the time of the authority or authorities cited. We are not consistent for reasons too involved to explain. The dangerous touchstones to personal pride should not enter the problematic lists. To be an author cited in this category implies no stigma for the following observations may explain it.

1. It may mean what a form was called before revisions determined otherwise. Possibly the name given was a large inclusive species or form now divided into several forms.

2. Species reduced in synonymy which need to be reexamined with more material.

3. Species introduced or accidental as *Crotalus atrox* in Wisconsin or *Cemophora coccinea* in Texas.

4. Species not yet well understood from lack of material (*Lampropeltis d. temporalis* and *Lampropeltis e. virginiana* before Conant 1943).

5. Species recorded in an adjoining state without or with barrier (e.g. east or west of Mississippi River) or with same general ecological attributes or in same zonal region.

6. Species of various hypothetical or extralimital lists (from DeKay, New York, 1842 to Guthrie, Iowa, 1926). The latter's list is also corrective.

7. Species in states where much has been done, written, etc. For example, the midwestern states of Indiana, Ohio, Michigan, Illinois, each have a problematic list almost as large as the accredited list. No one who knew O. P. Hay as we did would hold him not a good worker yet he appears frequently in our Indiana problematic list. The citations of Myers (Ind., 1926), Piatt (Ind., 1929) are usually corrections. In the same category fall

many recent workers in these lists. Taylor (Kansas, 1929), Conant (Ohio, 1938), Carr (Florida, 1940) and others in these lists are corrective.

8. Species mistakenly assigned to a state or province (e.g., *Natrix rigida* in Ontario).

9. Species puzzling in a state (*Natrix kirtlandii* in New Jersey).

10. Species extinct in a state (*Crotalus h. horridus* in Maine).

11. Species overlooked by herpetologists (*Tropidonotus obalskyi* in Canada).

12. Species which are truly doubtful, questionable or unsure records.

## STATE AND PROVINCE SPECIES LISTS

### Canada

1948 Mills, R. C. A Check List of the Reptiles and Amphibians of Canada. Herpetologica, Dec. 10, 1948. Vol. 4 Supplement 15 pp.

Species in Canada (37)

*Charina bottae*, B.C.
*Charina bottae utahensis*, B.C.
*Coluber c. constrictor*, N.S.; P.E.I.
*Coluber c. flaviventris*, Ont.
*Coluber c. mormon*, B.C.
*Contia mitis*, B.C.
*Crotalus h. horridus*, Ont.
*Crotalus v. oreganus*, B.C.
*Crotalus v. viridis*, Alta.; Sask.
*Diadophis p. edwardsi*, N.S.; Ont.; Que.
*Elaphe o. obsoleta*, Ont.
*Elaphe v. gloydi*, Ont.
*Heterodon platyrhinos*, Ont.
*Heterodon n. nasicus*, Man.; Sask.
*Lampropeltis d. triangulum*, N.B.; Ont.; Que.
*Natrix kirtlandii*, Ont.
*Natrix septemvittata*, Ont.
*Natrix s. insularum*, Ont.
*Natrix s. sipedon*, Ont.; Que.
*Opheodrys v. blanchardi*, Man.
*Opheodrys v. vernalis*, N.B.; Ont.; Que.
*Pituophis c. deserticola*, B.C.
*Pituophis c. sayi*, Alta.; Sask.
*Sistrurus c. catenatus*, Ont.
*Storeria d. dekayi*, N.B.; Ont.; Que.
*Storeria d. texana*, Man.
*Storeria d. wrightorum*, Ont.
*Storeria o. occipito-maculata*, Man.; N.B.; N.S.; Ont.; Cape Breton Id., P.E.I.; Que.
*Thamnophis e. vagrans*, Alta.; B.C.
*Thamnophis s. sirtalis*, N.B.; N.S.; Ont.; P.E.I.; Que.
*Thamnophis s. parietalis*, B.C.; Mack.; Man.; Ont.; Sask.
*Thamnophis s. pickeringii*, B.C.
*Thamnophis s. fitchi*, B.C.
*Thamnophis ordinoides*, B.C.
*Thamnophis r. butleri*, Ont.
*Thamnophis radix haydemi*, Man.; Sask.
*Thamnophis s. sauritus*, N.S.; Ont.; Que.

The garter snakes (*Thamnophis*) very fittingly end this list. The common garter snake (*T. s. sirtalis*) (see p. 603) in the five eastern provinces is the ubiquitous and predominant species of Canada as is the red-barred garter snake (*T. s. parietalis*) in five western provinces. The garters, nine in all recorded in Canada, make up one-fifth of the 37 species found in Canada. With their supposed relatives (*Natrix*, 4 and *Storeria*, 4) they constitute half (17) of the snake fauna of southern parts of Canada. The remaining 20 are scattered among the ten genera. Of these 20, one-half (11) occur only in Ontario and 7 species only in B. C., — that is, 16 of the 20 are in the Austral or prairie extensions into southern Ontario or in mild coastal extensions from Washington.

Viewed from point of view of numbers of forms in each province the table appears as follows.

Accredited Forms in each Province (35)

| | | | | | |
|---|---|---|---|---|---|
| Alta. | 5 | N.B. | 6 | Que. | 8 |
| B.C. | 12 | N.S. | 6 | Sask. | 6 |
| Mack. | 1 | Ont. | 20 | | |
| Man. | 6 | P.E.I. | 3 | | |

Problematic Forms in each Province (11)

| | | | | | |
|---|---|---|---|---|---|
| Alta. | 6 | N.B. | 4 | Que. | 1 |
| B.C. | 6 | N.S. | 4 | Sask. | 3 |
| Mack. | 0 | Ont. | 4 | | |
| Man. | 5 | P.E.I. | 3 | | |

Little more need be said in interpretation of the foregoing tables. Counting Ontario there is an average of 6.4 forms per province but a fairer average without Ontario would be 4.9 forms per province. The problematic list is more hypothetical or fluid but gives an average of 3.4 forms yet to be found or else eliminated from the consideration of each province. The four maritime provinces average 5.2 forms, have a paucity of snakes like New England. Much more exploration work needs to be done on them as well as the western provinces from Lake Superior to the British Columbia line.

### Alberta

I. Accredited
*Crotalus v. viridis*
*Pituophis s. sayi*
*Thamnophis e. vagrans*
*Thamnophis s. parietalis*
*Thamnophis r. haydeni*

II. Problematic (Hypothetical, Puzzling, Doubtful) Records
*Charina b. utahiensis*
*Coluber m. mormon*
*Diadophis p. arnyi*
*Opheodrys v. blanchardi*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*

### British Columbia

I. Accredited (12)
*Charina bottae*
*Coluber c. mormon*
*Contia mitis*
*Crotalus v. oreganus*
*Pituohis c. catenifer*
*Pituophis c. deserticola*
*Thamnophis e. nigricens*
*Thamnophis e. vagrans*
*Thamnophis s. pickeringii*
*Thamnophis s. fitchi*
*Thamnophis ordinoides*

II. Problematic (6)
*Crotalus v. viridis*
*Thamnophis o. biscutatus*
*Eutaenia leptocephala*
(Fannin 1898; Brown 1903)
*Pituophis c. sayi*
*Thamnophis s. trilineata*
(Cope 1893; Fitch 1941)
*Thamnophis s. concinna*
(Fannin 1898; Smith 1920; Patch 1922; Logier 1932; Vandenburgh 1937; Cowan 1937)

### Mackenzie

I. Accredited (1)
*Thamnophis s. parietalis*

II. Problematic

### Manitoba

I. Accredited (6)

*Heterodon n. nasicus*
*Opheodrys v. blanchardi*
*Opheodrys v. vernalis*
*Storeria o. occipitomaculata*
*Thamnophis s. parietalis*
*Thamnophis radix haydeni*

II. Problematic (5)

*Coluber c. flaviventris*
*Heterodon n. nasicus*
*Pituophis c. sayi*
*Storeria dekayi texana*
*Thamnophis sirtalis*

### New Brunswick

I. Accredited (6)

*Diadophis p. edwardsii*
*Lampropeltis d. triangulum*
*Opheodrys v. vernalis*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis sirtalis*

II. Problematic (4)

*Coluber c. constrictor* (Adams 1873)
*Crotalus h. horridus* (Adams 1873)
*Natrix s. sipedon* (Adams 1873)
*Diadophis p. edwardsii* (Adams 1873)

### Nova Scotia

I. Accredited (6)

*Coluber c. constrictor*
*Diadophis p. edwardsi*
*Opheodrys v. vernalis*
*Storeria o. occiptomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (4)

*Lampropeltis d. triangulum*
*Natrix s. sipedon*
*Opheodrys aestivus* (Verrill 1863)
*Thamnophis s. pallidula* (Allen 1899)

### Ontario

I. Accredited (20)

*Coluber c. flaviventris*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Elaphe o. obsoleta*
*Elaphe v. gloydi*
*Heterodon platyrhinos*
*Lampropeltis d. triangulum*
*Natrix kirtlandii*
*Natrix septemvittata*
*Natrix s. insularum*
*Natrix s. sipedon*
*Opheodrys v. vernalis*
*Sistrurus c. catenatus*
*Storeria d. dekayi*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. parietalis*
*Thamnophis r. butleri*
*Thamnophis s. sirtalis*

II. Problematic (4)

*Natrix e. erythrogaster* (Agassiz 1850)
*Natrix rigida* (Garnier 1881; (Nash 1908, LeRoy 1928)
*Thamnophis radix* (Nash 1908)
*Tropidonotus obalski* (Mocquard 1903; Garnier 1881)

### Prince Edward Island

I. Accredited (3)

*Coluber c. constrictor*
*Storeria o. occipitomaculata*
*Thamnophis sirtalis*

II. Problematic (3)

*Coluber lineatus* (Mellish 1875)
*Natrix s. sipedon*
*Opheodrys v. vernalis* (Mellish 1877; Cox 1899b)

## Quebec

I. Accredited (8)

*Diadophis p. edwardsii*
*Lampropeltis d. triangulum*
*Natrix s. sipedon*
*Opheodrys v. vernalis*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (1)

*Tropidonotus obalski* (Mocquard 1903)

## Saskatchewan

I. Accredited (6)

*Crotalus v. viridis*
*Opheodrys v. blanchardi*
*Pituophis s. sayi*
*Heterodon n. nasicus*
*Thamnophis radix haydeni*
*Thamnophis s. parietalis*

II. Problematic (3)

*Coluber c. flaviventris*
*Heterodon n. nascius*
*Thamnophis e. vagrans*

## United States and Lower California

1943 Stejneger L. and Barbour, T. A Check List of North American Amphibians and Reptiles. Fifth edition. Bull. Mus. Comp. Zool. Harvard Univ. Bull. XCIII No. 1 pp. XIX, 260

In United States there are now 287 recognized species and subspecies and in Lower California 74 forms recorded. The number of accredited forms and problematical forms for each state is herewith appended.

| | Accredited | Problematic | | Accredited | Problematic |
|---|---|---|---|---|---|
| Alaska | 1 | | Nebraska | 32 | 11 |
| Alabama | 55 | 12 | Nevada | 31 | 9 |
| Arizona | 75 | 20 | New Hampshire | 11 | 4 |
| Arkansas | 51 | 18 | New Jersey | 24 | 6 |
| California | 76 | 18 | New Mexico | 50 | 28 |
| Colorado | 24 | 14 | New York | 19 | 5 |
| Connecticut | 15 | 3 | North Carolina | 46 | 9 |
| Delaware | 18 | 7 | North Dakota | 9 | 6 |
| Dist. of Columbia | 23 | 6 | Ohio | 27 | 15 |
| Florida | 60 | 21 | Oklahoma | 66 | 10 |
| Georgia | 52 | 8 | Oregon | 24 | 8 |
| Idaho | 15 | 7 | Pennsylvania | 23 | 11 |
| Illinois | 49 | 17 | Rhode Island | 12 | 6 |
| Indiana | 33 | 28 | South Carolina | 48 | 8 |
| Iowa | 29 | 16 | South Dakota | 17 | 4 |
| Kansas | 47 | 17 | Tennessee | 45 | 15 |
| Kentucky | 40 | 13 | Texas | 92 | 27 |
| Louisiana | 50 | 14 | Utah | 31 | 9 |
| Maine | 10 | 4 | Vermont | 10 | 4 |
| Maryland | 26 | 9 | Virginia | 35 | 4 |
| Massachusetts | 14 | 5 | Washington | 17 | 7 |
| Michigan | 19 | 17 | West Virginia | 22 | 4 |
| Minnesota | 19 | 9 | Wisconsin | 24 | 10 |
| Mississippi | 43 | 13 | Wyoming | 13 | 9 |
| Missouri | 46 | 13 | | | |
| Montana | 10 | 8 | Lower California | 74 | 11 |

In numbers, our states and provinces roughly fall into the following groups according to numbers or accredited species (A) and accredited (A) plus

problematic (P) species added. Three of our most prideful states (Texas, California and Florida) are our most snaky states and are our herpetoolgists' paradise.

| | Accredited | Accredited plus Problematic |
|---|---|---|
| Alaska, Mackenzie | A 1 | |
| N.S. to Alberta (less Ontario) | A 3-8 | A+P 6-10 |
| New England | A 10-15 | A+P 13-19 |
| N.D., S.D., Mont., Wyo. | A 9-17 | A+P 14-19 |
| B.C., Wash., Ore. | A 12-24 | A+P 18-32 |
| Ida., Nev., Utah, Colo. | A 15-31 | A+P 22-40 |
| Middle Atlantic States to Va., Ont., Great Lakes States exc. Ind., Ill., Iowa | A 18-35 | A+P 24-42 |
| Neb., Kan., Mo., Ill., Ind., Ky., Tenn. | A 33-49 | A+P 43-66 |
| N.C., S.C., Ga., Ala., Ark., Miss., La. | A 43-52 | A+P 56-69 |
| Florida | A 60 | A+P 81 |
| Cal., L.C., Ariz., N.M. | A 50-76 | A+P 78-95 |
| Okla. | A 64 | A+P 76 |
| Texas | A 92 | A+P 119 |

Sixteen states need much more exploration of their amphibians and reptiles. They are: Alabama, Arkansas, Colorado, Idaho, Iowa, Kentucky, Mississippi, Missouri, Montana, Nebraska, New Mexico, North Dakota, South Dakota, Tennessee, West Virginia and Wyoming.

## Alabama

I. Accredited (55)

*Abastor erythrogrammus*
*Agkistrodon c. contortrix*
*Agkistrodon c. mokeson*
*Agkistrodon p. leucostoma*
*Agkistrodon p. piscivorus*
*Carphophis a. amoena*
*Carphophis a. helenae*
*Cemophora coccinea*
*Coluber c. constrictor*
*Crotalus adamanteus*
*Crotalus h. atricaudatus*
*Crotalus h. horridus*
*Diadophis p. punctatus*
*Diadophis p. stictogenys*
*Drymarchon c. couperi*
*Elaphe guttata*
*Elaphe o. confinis*
*Farancia a. abacura*
*Farancia a. reinwardtii*
*Haldea striatula*
*Haldea v. elegans*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Heterodon simus*
*Lampropeltis d. doliata*
*Lampropeltis g. getulus*
*Lampropeltis g. holbrooki*
*Lampropeltis g. nigra*
*Lampropeltis rhombomaculata*
*Masticophis f. flagellum*
*Micrurus f. fulvius*
*Natrix clarkii*
*Natrix c. cyclopion*
*Natrix e. erythrogaster*
*Natrix e. flavigaster*
*Natrix rhombifera*
*Natrix rigida*
*Natrix septemvittata*
*Natrix s. fasciata*
*Natrix s. pleuralis*
*Natrix s. sipedon* (Dunn 19
*Natrix taxispilota*
*Opheodrys aestivus*
*Pituophis m. lodingi*
*Rhadinea flavilatus*
*Sistrurus m. barbouri*
*Sistrurus m. miliarius*
*Sistrurus m. streckeri*
*Storeria d. dekayi*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Tantilla c. coronata*
*Thamnophis s. sackenii*
*Thamnophis s. sirtalis*
*Thamnophis s. sauritus*

II. Problematic (11)

*Coluber o. lemniscatus*
(Cope 1889)
*Coluber spiloides*
(Cope 1900)
*Diadophis h. edwardsii*
*Drymarchon c. erebennus*
*Elaphe o. obsoletus*
(Garman 1884; Loding 1922; Haltom 1931 Sprout River, Ark. not Ala.)
*Elaphe quadrivittata*
(Loding 1922)
*Lampropeltis t. amaura*
*Natrix kirtlandi*
(Loding 1927; Haltom 1931)

*Natrix s. confluens*
*Pituophis m. melanoleucus*
(A.H.W.)
*Pituophis m. mugitus*
*Sistrurus c. catenatus*
(Loding 1922; Haltom 1931; Gloyd 1940)

## Alaska

I. Accredited (1)
*Thamnophis* (Williams 1925: 72)

## Arizona

I. Accredited (75)

*Arizona e. eburnata*
*Arizona e. noctivaga*
*Arizona e. philipi*
*Chilomeniscus cinctus*
*Chionactis o. annulata*
*Chionactis o. klauberi*
*Chionactis o. occipitalis*
*Chionactis o. organica*
*Chionactis o. talpina*
(intergrades)
*Coluber c. mormon*
*Crotalus atrox*
*Crotalus cerastes cerastes*
*Crotalus c. laterorepens*
*Crotalus m. pyrrhus*
*Crotalus m. molossus*
*Crotalus l. klauberi*
*Crotalus scutulatus*
*Crotalus tigris*
*Crotalus t. pricei*
*Crotalus v. abyssus*
*Crotalus v. cerberus*
*Crotalus v. lutosus*
*Crotalus v. nuntius*
*Crotalus v. viridis*
*Crotalus willardi*
*Diadophis r. laetus*
*Diadophis r. regalis*
*Elaphe chlorosoma*
*Gyalopion canum*
*Heterodon n. kennerlyi*
*Hypsiglena t. ochrorhynchus*
*Hypsiglena t. deserticola*
*Lampropeltis d. gentilis*
*Lampropeltis g. californiae*
(*boylii*)
*Lampropeltis g. splendida*
*Lampropeltis g. yumensis*
*Lampropeltis pyromelaena*
*Leptotyphlops d. dissectus*
*Leptotyphlops h. cahuilae*
*Leptotyphlops h. humilis*
*Leptotyphlops h. segregus*
*Lichanura r. gracia*
*Masticophis bilineatus*
*Masticophis b. lineolatus*
*Masticophis f. frenatus*
(*piceus*)
*Masticophis f. frenatus*
*Masticophis t. taeniatus*
*Micruroides euryxanthus*
*Oxybelis microphthalmus*
*Phyllorhynchus b. browni*
*Phyllorhynchus b. lucidus*
*Phyllorhynchus d. nubilus*
*Phyllorhynchus d. perkinsi*
*Pituophis c. affinis*
*Pituophis c. deserticola*
*Rhinocheilus l. clarus*
*Rhinocleilus l. lecontii*
*Salvadora g. grahamiae*
*Salvadora h. deserticola*
*Salvadora h. hexalepis*
*Salvadora h. mohavensis*
*Sistrurus c. tergeminus*
*Sonora s. gloydi*
*Sonora s. isozona*
*Sonora s. linearis*
*Sonora s. semiannulata*
*Tantilla atriceps*
*Tantilla nigriceps*
*Tantilla wilcoxi*
*Thamnophis eques cyrtopsis*
*Thamnophis e. megalops*
*Thamnophis e. vagrans*
*Thamnophis marcianus*
*nigrolateris*
*Thamnophis s. parietalis*
*Thamnophis rufipunctatus*
*Trimorphodon lamba*

II. Problematic

*Caudisona l. cerberus*
(Coues 1875; Garman 1884)
*Caudisona lecontei*
(Cope 1866)
*Coluber lateralis*
(Mearns 1907)
*Coluber c. mormon*
(some records)
*Crotalus ruber*
(Noguchi 1909)
*Diadophis a. pulchellus*
(Yarrow 1875)
*Diadophis docilis*
(Baird 1859; Mearns 1907)
*Elaphe emoryi intermontana*
*Heterodon n. nascicus*
*Lampropeltis d. annulatus*
(Yarrow 1875)
*Lampropeltis g. conjuncta*
(Cope 1862; Vandenburgh 1912a; Vandenburgh and Slevin 1913)
*Lampropeltis p. celaenops*
Stejneger 1903; etc.)
*Leptodeira septentrionalis*
(Coues 1875; Garman 1884; Noguchi 1909)
*Lichanura trivirgata*
(Werner 1921)
*Natrix valida*
*Pituophis s. mexicanus*
(Yarrow 1875)
*Sistrurus miliarius*
Coues 1875)
*Tantilla coronata*
(Vandenburgh 1897)
*Thamnophis hammondi*
(Brown 1903)
*Trimorphodon lyrophanes*

## Arkansas

I. Accredited (51)

*Agkistrodon c. contortrix*
*Agkistrodon c. mokeson*
*Agkistrodon p. leucostoma*
*Carphophis a. vermis*
*Cemophora coccinea*
*Coluber c. constrictor*
*Coluber c. flaviventris*
*Crotalus atrox*
*Crotalus h. atricaudatus*
*Crotalus h. horridus*
*Diadophis p. arnyi*
*Diadophis p. stictogenys*
*Elaphe e. emoryi*
*Elaphe guttata*
*Elaphe o. confinis*
*Elaphe o. obsoleta*
*Farancia a. reinwardtii*
*Haldea striatula*
*Haldea v. elegans*
*Heterodon platyrhinos*
*Lampropeltis calligaster*
*Lampropeltis g. holbrooki*
*Lampropeltis g. nigra*
*Lampropeltis d. amaura*
*Lampropeltis d. syspila*
*Masticophis f. flagellum*
*Micrurus f. tenere*
(Schmidt & Davis 1941)
*Natrix c. cyclopion*
*Natrix e. flavigaster*
*Natrix e. transversa*
*Natrix grahami*
*Natrix rhombifera*
*Natrix septemvittata*
*Natrix s. confluens*
*Natrix s. fasciata*
*Natrix s. pleuralis*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. blanchardi*
*Pituophis c. sayi*
*Sistrurus m. streckeri*
*Storeria d. wrightorum*
*Storeria d. texana*
*Storeria o. occipitomaculata*
*Tantilla gracilis gracilis*
*Tantilla gracilis hallowelli*
*Thamnophis eques cyrtopsis*
*Thamnophis s. sirtalis*
*Thamnophis s. parietalis*
*Thamnophis r. radix*
*Thamnophis s. proximus*
*Tropidoclonion lineatum*

II. Problematic (20)

*Coluber c. constrictor*
*Coluber spiloides*
(Hurter and Strecker 1909)
*Crotalus adamanteus*
(Yarrow 1882; Hurter and Strecker 1909)
*Crotalus v. viridis*
(Yarrow 1882; Trecul 1876; Baird and Girard 1854)
*Diadophis p. edwardsii*
(Schwardt 1938)
*Elaphe guttata*
(Evans 1940)
*Elaphe o. confinis*
*Elaphe o. lindheimeri*
(Davis and Rice 1883)
*Heterodon nasicus*
(Hallowell 1857)
*Lampropeltis t. gentilis*
(Jan 1863; Higgins 1873; Garman 1884)
*Micrurus fulvius*
(Yarrow 1882; Hurter and Strecker 1909)
*Natrix e. neglecta*
*Natrix rigida*
(Strecker and Williams 1928)
*Natrix s. fasciata*
(Strecker 1908; Strecker and Hurter 1909; Perkins 1928)
*Opheodrys v. blanchardi*
(Hurter and Strecker 1909)
*Opheodrys v. vernalis*
(Hurter 1909; Grobman 1941)
*Thamnophis eques cyrtopsis*
(Strecker 1908; Hurter and Strecker 1909)
*Thamnophis s. sauritus*
(Perkins and Lentz 1934)
*Thamnophis s. sackenii*
(McLain 1899)
*Tropidonotus woodhousii*
(Jan 1864-5)

## California

I. Accredited (77)

*Arizona e. candida*
*Arizona e. eburnata*
*Arizona e. occidentalis*
*Charina bottae*
*Charina b. umbratica*
*Charina b. utahensis*
*Chilomeniscus cinctus*
*Chionactis o. annulata*
*Chionactis o. occipitalis*
*Chionactis o. talpina*
(intergrades)
*Coluber c. mormon*
*Contia tenuis*
*Crotalus atrox*
*Crotalus c. cerastes*
*Crotalus c. laterorepens*
*Crotalus m. pyrrhus*
*Crotalus m. stephensi*

*Crotalus ruber*
*Crotalus scutulatus*
*Crotalus v. helleri*
*Crotalus v. lutosus*
*Crotalus v. oreganus*
*Diadophis a. amabilis*
*Diadophis a. modestus*
*Diadophis a. occidentalis*
*Diadophis a. pulchellus*
*Diadophis a. similis*
*Diadophis a. vandenburghii*
*Hypsiglena t. deserticola*
*Hypsiglena t. klauberi*
*Hypsiglena t. nuchulatus*
*Lampropeltis g. californiae*
*Lampropeltis g. californiae* (*boylii*)
*Lampropeltis g. yumensis*
*Lampropeltis z. multicincta*
*Lampropeltis z. zonata*
*Leptotyphlops h. cahuilae*
*Leptotyphlops h. humilis*
*Lichanura r. gracia*
*Lichanura r. roseofusca*
*Masticophus lateralis*
*Masticophus piceus* (*frenatus*)
*Masticophus piceus* (*piceus*)
*Masticophus t. taeniatus*
*Phyllorrhynchus d. perkinsi*
*Pituophis c. affinis*
*Pituophis c. annectans*
*Pituophis c. catenifer*
(*Pituophis c. heermanni*)
*Rhinocheilus l. clarus*
*Rhinocheilus l. lecontei*
*Salvadora h. hexalepis*
*Salvadora h. mohavensis*
*Salvadora h. virgultea*
*Sonora m. linearis*
*Sonora s. semiannulata*
*Tantilla eiseni*
*Tantilla e. transmontana*
*Tantilla utahiensis*
*Thamnophis e. aquaticus*
*Thamnophis e. atratus*
*Thamnophis e. biscutatus*
*Thamnophis e. couchi*
*Thamnophis e. elegans*
*Thamnophis e. gigas*
*Thamnophis e. hammondi*
*Thamnophis e. hydrophila*
*Thamnophis e. terrestris*
*Thamnophis e. vagrans*
*Thamnophis m. nigrolateris*
*Thamnophis ordinoides*
*Thamnophis s. fitchi*
*Thamnophis s. infernalis*
*Thamnophis s. tetrataenia*
*Trimorphodon lambda*
*Trimorphodon vandenburghii*

II. Problematic (18)

*Conopsis nasus* (Gunther 1858; Garman 1884)
*Crotalus hallowelli* (Cooper 1869)
*Crotalus lecontei* (Hallowell-Heermann 1853)
*Crotalus v. viridis* (Mearns 1907)
*Heterodon nasicus* (Higgins 1873; Garman 1884)
*Lampropeltis g. conjuncta* (Hall and Grinnell 1919)
*Lampropeltis pyromelaena* (Mearns 1907)
*Lichanura trivirgata* (Werner 1921)
*Natrix valida* (Cope 1862)
*Pituophis d. deppei* (Stull 1940)
*Pituophis melanoleucas* (Jan 1863)
*Pituophis s. affinis* (Stull 1940)
*Pituophis vertebralis* (Blainville 1835; Jan 1863; Stull 1932)
*Thamnophis e. megalops*
*Thamnophis obscura* (Townsend 1888)
*Thamnophis s. pickeringii* (Townsend 1888)
*Thamnophis s. sirtalis* (Townsend 1888)
*Tropidonotus ordinata* (Hallowell 1853)

## Colorado

I. Accredited (24)

*Arizona e. blanchardi*
*Coluber c. flaviventris*
*Coluber f. flavigularis*
*Crotalus atrox*
*Crotalus v. concolor ?*
*Crotalus v. viridis*
*Diadophis p. arnyi*
*Elaphe l. intermontana*
*Heterodon n. nasicus*
*Hypsiglena t. lorealus*
*Lampropeltis t. gentilis*
*Natrix s. sipedon*
*Opheodrys v. blanchardi*
*Pituophis c. deserticola*
*Pituophis c. affinis*
*Pituophis c. sayi*
*Rhinocheilus l. tessellatus*
*Sistrurus c. tergeminus*
*Sonora episcopa*
*Tantilla nigriceps*
*Thamnophis e. cryptopsis*
*Thamnophis e. vagrans*
*Thamnophis s. parietalis*
*Thamnophis radix haydeni*
*Thamnophis s. proximus*
*Tropidodonion lineatum*

II. Problematic (14)

*Ablabes o. occipitalis*
(Cope 1861)
*Crotalus atrox*
(Ellis and Henderson 1910)
*Crotalus lecontei*
(Hallowell 1854)
*Diadophis r. regalis*
(Cope 1898; Ellis and Henderson 1913)
*Heterodon platyrhinos*
*Hypsiglena t. texana*
*Lampropeltis g. holbrooki*
*Natrix s. fasciata*
(Ellis and Henderson 1915)
(Ellis and Henderson 1910)
*Crotalus cerastes*
*Storeria dekayi*
(Ellis and Henderson 1913)
*Thamnophis megalops*
(Ellis and Henderson 1910, 1913, 1915; Henshaw 1873)
*Thamnophis marcianus nigrolateris*
(Yarrow 1875, 1875a)
*Thamnophis s. dorsalis*
(Yarrow 1875)

## Connecticut

I. Accredited (15)

*Agkistrodon c. mokeson*
*Carphophis a. amoena*
*Coluber c. constrictor*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Elaphe o. obsoleta*
*Heterodon platyrhinos*
*Lampropeltis d. triangulum*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. vernalis*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis s. sirtalis*
*Thamnophis s. sauritus*

II. Problematic (3)

*Lampropeltis g. getulus*
(Henshaw 1904)
*Natrix e. erythrogaster*
Henshaw 1904)
Stejneger 1904)
*Natrix septemvittata*
(Henshaw 1904)

## Delaware

I. Accredited (18)

*Agkistrodon m. mokeson*
*Carphophis a. amoena*
*Coluber c. constrictor*
*Crotalus h. horridus*
*Diadophis p. punctatus*
*Elaphe g. guttata*
*Elaphe o. obsoleta*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Lampropeltis g. getulus*
*Lampropeltis d. temporalis*
*Lampropeltis d. triangulum*
*Natrix septemvittata*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Storeria d. dekayi*
*Thamnophis s. sirtalis*
*Thamnophis s. sauritus*

II. Problematic (7)

*Cemophora coccinea*
*Crotalus h. atricaudatus*
*Diadophis p. edwardsii*
(See Conant 1946)
*Natrix e. erythrogaster*
*Opheodrys v. vernalis*
*Pituophis melanoleucas*
(Wallace 1904)
*Storeria o. occipitomaculata*

## District of Columbia

I. Accredited (23)

*Agkistrodon c. mokeson*
*Carphophis a. amoena*
*Cemophora coccinea*
*Coluber c. constrictor*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Elaphe guttata*
*Elaphe o. obsoleta*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Lampropeltis g. getulus*
*Lampropeltis c. rhombomaculata*
*Lampropeltis d. temporalis*
*Lampropeltis d. triangulum*
*Natrix septemvittata*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. vernalis*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (6)

*Crotalus h. atricaudatus*
*Diadophis p. punctatus*
*Lampropeltis d. virginiana*
*Lampropeltis d. temporalis*
*Natrix bisecta*
(Cope 1887, 1888; Hay 1892; Hay 1902, McAtee 1918)
*Natrix taxispilota*
(Yarrow 1883; Cope 1900; Ditmars 1936)

## Florida

I. Accredited (60)

*Abastor erythrogrammus*
*Agkistrodon c. contortrix*
*Agkistrodon p. piscivorus*
*Carphophis a. amoena*
*Cemophora coccinea*
*Coluber c. constrictor*
*Coluber c. priapus*
*Crotalus adamanteus*
*Crotalus h. atricaudatus*
*Diadophis p. punctatus*
*Drymarchon c. couperi*
*Elaphe guttata*
*Elaphe g. rosacea*
*Elaphe o. confinis*
*Elaphe o. deckerti*
*Elaphe o. quadrivittata*
*Elaphe o. rossalleni*
*Elaphe o. williamsi*
*Farancia a. abacura*
*Farancia a. reinwardtii*
*Haldea striatula*
*Haldea v. valeriae*
*Heterodon p. browni*
*Heterodon p. platyrhinos*
*Heterodon simus*
*Lampropeltis d. doliata*
*Lampropeltis d. triangulum*
*Lampropeltis g. brooksi*
*Lampropeltis g. floridana*
*Lampropeltis g. getulus*
*Lampropeltis g. goini*
*Lampropeltis c. rhombomaculata*
*Liodytes alleni*
*Liodytes a. lineapiatus*
*Masticophis f. flagellum*
*Micrurus f. barbouri*
*Micrurus f. fulvius*
*Natrix c. cyclopion*
*Natrix c. floridana*
*Natrix e. erythrogaster*
*Natrix rigida*
*Natrix s. clarki*
*Natrix s. compressicauda*
*Natrix s. fasciata*
*Natrix s. pictiventris*
*Natrix s. taeniata*
*Natrix taxispilota*
*Opheodrys aestivus*
*Pituophis m. mugitus*
*Rhadinea flavilata*
*Seminatrix pygaea pygaea*
*Seminatrix p. cyclas*
*Sistrurus m. barbouri*
*Stilosoma extenuatum*
*Storeria d. victa*
*Storeria d. wrightorum*
*Storeria o. obscura*
*Tantilla c. coronata*
*Tantilla c. wagneri*
*Thamnophis s. sirtalis*
*Thamnophis s. sackenii*

II. Problematic (21)

*Diadophis p. stictogenys*
*Elaphe o. obsoleta* (Carr 1940)
*Elaps distans* (Cope 1875; Yarrow 1882; Davis & Rice 1883)
*Haldea v. elegans*
*Lampropeltis t. amaura* (Deckert 1918)
*Lampropeltis t. parallelus* (Cope 1889)
*Lampropeltis t. syspila* (Cope 1889)
*Lampropeltis d. triangulum*
*Leptotyphlops dulcis* (Werner 1917)
*Micrurus f. tenere* (Yarrow 1882)
*Natrix compressicauda* complex
*walkeri* (Cope 1889)
*compsolaernia* (Cope 1889)
*bivittata* (Cope 1889)
*taeniata* (Cope 1895)
*usta* (Cope 1889)
*Natrix septemvittata*
*Opheodrys v. vernalis* (Cope 1898; Carr 1940; Grobman 1941)
*Ophthalmidion longissima* (Higgins 1873)
*Pituophis melanoleucas*
*Thamnophis s. sauritus* (Deckert 1918)

## Georgia

I. Accredited (52)

*Abastor erythrogrammus*
*Agkistrodon c. contortrix*
*Agkistrodon c. mokeson*
*Agkistrodon p. piscivorus*
*Carphophis a. amoena*
*Cemophora coccinea*
*Columber c. constrictor*
*Crotalus adamanteus*
*Crotalus h. atricaudatus*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Diadophis p. punctatus*
*Drymarchon c. couperi*
*Elaphe guttata*
*Elaphe o. confinis*
*Elaphe o. obsoleta*
*Elaphe o. quadrivittata*
*Farancia a. abacura*
*Haldea striatula*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Heterodon simus*
*Lampropeltis c. rhombomaculata*
*Lampropeltis d. doliata*
*Lampropeltis g. getulus*
*Lampropeltis d. triangulum*
*Liodytes alleni*
*Masticophis f. flagellum*
*Micrurus f. fulvius*
*Natrix c. floridana*
*Natrix e. erythrogaster*
*Natrix rigida*

*Natrix septemvittata*
*Natrix s. fasciata*
*Natrix s. pleuralis*
*Natrix s. sipedon*
*Natrix taxispilota*
*Opheodrys aestivus*
*Pituophis melanoleucas*
*Pituophis m. mugitus*
*Rhadinea flavilata*
*Seminatrix pygaea*
*Sistrurus m. barbouri*
*Sistrurus m. miliarius*
*Storeria d. victa*
*Storeria d. wrightorum*
*Storeria o. obscura*
*Storeria o. occipitomaculata*
*Tantilla c. coronata*
*Thamnophis s. sirtalis*
*Thamnophis s. sackeni*
*Thamnophis s. sauritus*

II. Problematic (8)
*Coluber c. priapus*
*Coluber o. lemniscatus*
(Cope 1889)
*Diadophis p. stictogenys*
(Cope 1898-1900)
(Jan 1863)
*Farancia a. reinwardtii*
*Heterodon nasicus*
(Jan 1863-4)
*Lampropeltis g. nigra*
*Storeria d. victa*
*Sistrurus c. catenatus*
(Yarrow 1882; Davis and Rice 1883; Gloyd 1940)

## Idaho

I. Accredited (15)
*Charina bottae utahensis*
*Coluber c. mormon*
*Crotalus v. lutosus*
*Crotalus v. oreganus*
*Crotalus v. viridis*
*Diadophis a. occidentalis*
*Diadophis r. regalis*
*Hypsiglena t. deserticola*
*Masticophis t. taeniatus*
*Pituophis c. deserticola*
*Rhinocheilus l. lecontei*
*Sonora s. isozona*
*Thamnophis e. vagrans*
*Thamnophis s. parietalis*
*Thamnophis s. tetrataenia*

II. Problematic (7)
*Opheodrys v. blanchardi*
*Pituophis c. catenifer*
(Vandenburgh 1912b)
*Pituophis c. stejnegeri*
(Vandenburgh 1920 +)
*Pituophis c. sayi*
*Thamnophis e. biscutatus*
*Thamnophis s. concinna*
*Thamnophis s. pickeringii*

## Illinois

I. Accredited (49)
*Agkistrodon d. contortrix*
*Agkistrodon d. mokesen*
*Agkistrodon p. leucostoma*
*Carphophis a. helenae*
*Carphophis a. vermis*
*Coluber c. flaviventris*
*Crotalus h. atricaudatus*
*Crotalus h. horridus*
*Diadophis p. arnyi*
*Diadophis p. edwardsii*
*Diadophis p. stictogenys*
*Elaphe e. emoryi*
*Elaphe o. obsoleta*
*Elaphe v. vulpina*
*Farancia a. reinwardtii*
*Haldea striatula*
*Haldea v. elegans*
*Heterodon n. nasicus*
*Heterodon platyrhinos*
*Lampropeltis d. syspila*
*Lampropeltis d. triangulum*
*Lampropeltis g. holbrooki*
*Lampropeltis g. nigra*
*Micrurus f. fulvius*
*Lampropeltis calligaster*
*Natrix c. cyclopion*
*Natrix e. flavigaster*
*Natrix e. neglecta*
*Natrix grahami*
*Natrix kirtlandii*
*Natrix rhombifera*
*Natrix septemvittata*
*Natrix s. confluens*
*Natrix s. pleuralis*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. blanchardi*
*Pituophis c. sayi*
*Sistrurus c. catenatus*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Tantilla gracilis hallowelli*
*Thamnophis s. sirtalis*
*Thamnophis s. parietalis*
*Thamnophis r. butleri*
*Thamnophis r. radix*
*Thamnophis s. proximus*
*Thamnophis s. sauritus*
*Tropidoclonio lineatum*

II. Problematic (17)
*Abastor erythrogrammus*
(Garman 1883; Davis and Rice 1883)
*Carphophis a. vermis*
*Coluber c. constrictor*
(Hankinson 1917; Blanchard 1925; Van Cleave 1925)
*Coluber spiloides*
(McLain 1899)
*Elaphe guttata*
(Davis & Rice 1883; Hay 1892; Myers 1926; Van Cleave 1928)
*Elaphe o. confinis*
*Elaphe lindheimeri*
(Garman 1884; Davis and Rice 1883; H. Garman 1892)
*Haldea striatula*

(Garman 1892; Van Cleave 1928)
*Haldea v. valeriae*
Garman 1892)
*Heterodon simus*
(Garman 1892)
*Lampropeltis rhombomaculata*
(Davis & Rice 1883)
*Lampropeltis e. elapsoides*
(Garman 1892)
*Natrix e. transversa*
(Davis & Rice 1883; Hurter 1893)
*Natrix rigida*
(Hay 1892; McLain 1899)
*Natrix s. fasciata*
(Garman 1893; Gaige 1914)
*Thamnophis e. vagrans*
(Nelson-Garman 1892)
*Tropidonotus hammondi*
(Jan 1864-5)

**Indiana**

I. Accredited (33)

*Agkistrodon c. mokeson*
*Carphophis a. helenae*
*Coluber c. constrictor*
*Coluber c. flaviventris*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Elaphe o. obsoleta*
*Elaphe v. vulpina*
*Farancia a. reinwardtii*
*Haldea v. elegans*
*Heterodon platyrhinos*
*Heterodon n. nasicus*
*Lampropeltis calligaster*
*Lampropeltis d. syspila*
*Lampropeltis d. triangulum*
*Lampropeltis g. nigra*
*Micrurus f. fulvius*
*Natrix e. neglecta*
*Natrix kirtlandii*
*Natrix rhombifera*
*Natrix septemvittata*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. blanchardi*
*Pituophis c. sayi*
*Sistrurus c. catenatus*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis r. butleri*
*Thamnophis r. radix*
*Thamnophis s. proximus*
*Thamnophis s. sirtalis*

II. Problematic

*Abastor erythrogrammus*
(Hay 1892)
*Agkistrodon p. leucostoma*
(Hay 1892; Gaines 1924a; Myers 1926; Piatt 1930; Blatchley; Swanson 1939)
*Carphophis a. vermis*
(Yarrow 1883; Hay 1892)
*Coluber spiloides*
(Cope 1900)
*Diadophis p. arnyi*
(Piatt 1930; Gaines 1924a)
*Diadophis p. stictogenys*
(Myers 1926; Piatt 1930)
*Diadophis punctatus*
(Blatchley 1891)
*Elaphe guttata*
(Hughes 1886; Yarrow; Hay 1892; Gaines 1924b; McAtee 1907; Myers 1926)
*Elaphe o. confinis*
(Blatchley-Hay 1892; Blanchard 1925; Myers 1926)
*Elaphe o. lindheimeri*
(Boulenger 1894)
*Elaphe laeta*
(Yarrow, Hughes 1886; Hay 1887)
*Eutaenia radix melanotaenia*
(Cope 1889)
*Haldea striatula*
(Hay 1892; Piatt 1930)
*Lampropeltis e. elapsoides*
(Myers 1926; Piatt 1931)
*Lampropeltis g. holbrooki*
(Hay 1892; Myers 1926; Piatt 1930)
*Micrurus f. fulvius*
(Hay 1892)
*Natrix c. cyclopion*
(Hay 1892; Piatt 1930)
*Natrix grahami*
(Piatt 1930)
*Natrix rigida*
(Hay 1892)
*Natrix s. confluens*
*Natrix s. fasciata*
(Hay 1887, 1892; McAtee 1907)

*Natrix s. pleuralis*
(Clay 1938)
*Pituophis melanoleucas*
(Hay 1892)
*Thamnophis radix* or *O. elegans*
(U.S.N.M.U. Go. Co. Ind.)
*Thamnophis s. proximus*
(Hay 1892)
*Thamnophis s. parietalis*
(Hay 1887; Hay 1892)
*Tropidoclonion lineatum*
(Hay 1892; Myers 1926; Piatt 1930)
*Virginia valeriae*
(Hay 1892)

## Iowa

I. Accredited (29)

*Agkistrodon c. mokeson*
*Carphophis a. vermis*
*Coluber c. flaviventris*
*Crotalus h. horridus*
*Diadophis p. arnyi*
*Elaphe e. emoryi*
*Elaphe o. obsoleta*
*Elaphe v. vulpina*
*Haldea v. elegans*
*Heterodon platyrhinos*
*Heterodon n. nasicus*
*Lampropeltis calligaster*
*Lampropeltis d. syspila*
*Lampropeltis g. holbrooki*
*Natrix grahami*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. blanchardi*
*Pituophis c. sayi*
*Sistrurus c. catenatus*
*Storeria d. texana*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Thamnophis s. sirtalis*
*Thamnophis s. parietalis*
*Thamnophis radix*
*Thamnophis r. haydeni*
*Thamnophis s. proximus*
*Tropidoclonion lineatum*

II. Problematic (16)

*Agkistrodon p. leucostoma*
(Somes 1911; Guthrie 1926)
*Coluber c. constrictor*
(Somes 1911; Ruthven 1912; Guthrie 1926)
*Crotalus v. viridis*
(Somes 1911; Guthrie 1926)
*Diadophis p. edwardsii*
(Guthrie 1926)
*Diadophis p. stictogenys*
(Guthrie 1926)
*Elaphe guttata*
(Guthrie 1926)
*Haldea striatula*
(Guthrie 1926; Breckenridge 1937)
*Lampropeltis g. getulus*
(Guthrie 1926)
*Lampropeltis t. triangulum*
(Somes 1911; Guthrie 1926)
*Natrix e. erythrogaster*
(Somes 1911; Guthrie 1926)
*Natrix kirtlandii*
(Guthrie 1926)
*Natrix rigida*
(Osborn 1892; Somes 1911; Guthrie 1926)
*Natrix septemvittata*
(Somes 1911; Guthrie 1926)
*Natrix s. sauritus*
(Somes 1911; Guthrie 1926)
*Natrix s. fasciata*
(Somes 1911; Guthrie 1926)
*Thamnophis s. sauritus*
(Somes 1911; Guthrie 1926)

## Kansas

I. Accredited (47)

*Agkistrodon c. contortrix*
*Agkistrodon c. laticinctus*
*Agkistrodon p. leucostoma*
*Arizona e. blanchardi*
*Carphophis a. vermis*
*Coluber c. flaviventris*
*Crotalus atrox*
*Crotalus h. horridus*
*Crotalus v. viridis*
*Diadophis p. arnyi*
*Elaphe e. intermontana*
*Elaphe e. emoryi*
*Elaphe o. obsoleta*
*Haldea v. elegans*
*Haldea striatula*
*Heterodon n. nasicus*
*Heterodon platyrhinos*
*Hypsiglena t. texana*
*Lampropeltis calligaster*
*Lampropeltis d. gentilis*
*Lampropeltis d. syspila*
*Lampropeltis g. holbrooki*
*Leptotyphlops d. dissectus*
*Masticophis f. flagellum*
*Masticophis f. flavigularis*
*Natrix e. flavigaster*
*Natrix e. transversa*
*Natrix grahami*
*Natrix rhombifera*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. blanchardi*
*Pituophis c. sayi*
*Rhinocheilus l. tessellatus*
*Sistrurus c. catenatus*
*Sistrurus c. tergeminus*
*Sonora episcopa*
*Storeria d. texana*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Tantilla gracilis hallowelli*
*Tantilla nigriceps*
*Thamnophis marcianus nigrolateris*
*Thamnophis s. parietalis*
*Thamnophis radix haydeni*
*Thamnophis s. proximus*
*Tropidoclonion lineatum*

II. Problematic (17)

*Coluber spiloides*
Branson 1904; Hurter 1911; Taylor 1929a)
*Diadophis p. docilis*
(Popenow; Cragin 1881)
*Diadophis r. regalis*
(Branson 1904; Burt 1927; Taylor 1929a)
*Elaphe o. confinis*
(Hallowell 1857; Cragin 1881)
*Elaphe v. vulpina*
(Cope; Cragin; Branson; Taylor 1929)
*Eutaenia e. vagrans*
(Nolan; Garman; Branson 1904; Taylor 1929a)
*Heterodon simus*
(Mozley 1878; Branson 1904)
*Lampropeltis d. amaura*
(Mozley; Cragin 1881)
*Lampropeltis d. triangulum*
(Branson 1904; Taylor 1929a)
*Leptotyphlops myopica*
(Tihen 1938; Taylor 1939)
*Natrix s. fasciata*
(Dice 1923; Linsdale 1927)
*Thamnophis o. ordinoides*
(Nolan; Cragin 1881; Branson 1904)
*Thamnophis s. sauritus*
(Mozley 1878; Cragin 1881; Branson 1904)
*Thamnophis s. obscura*
(Cragin 1885)
*Thamnophis s. ordinata*
(Hammond; Nolan)
*Thamnophis s. pickeringii*
(Cragin 1885)
*Thamnophis s. sirtalis*
(Mozley 1878; Cragin 1881; Branson 1904; Taylor 1929a)

**Kentucky**

I. Accredited (40)

*Agkistrodon c. contortrix*
*Agkistrodon c. mokeson*
*Agkistrodon p. leucostoma*
*Carphophis a. amoena*
*Carphophis a. helenae*
*Cemophora coccinea*
*Coluber c. constrictor*
*Crotalus h. atricaudatus*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Diadophis p. stictogenys*
*Elaphe guttata*
*Elaphe o. confinis*
*Elaphe o. obsoleta*
*Elaphe v. vulpina*
*Farancia a. reinwardtii*
*Haldea v. elegans*
*Haldea p. valeriae*
*Heterodon platyrhinos*
*Lampropeltis calligaster*
*Lampropeltis d. doliata*
*Lampropeltis d. syspila*
*Lampropeltis d. triangulum*
*Lampropeltis g. holbrooki*
*Lampropeltis g. niger*
*Masticophis f. flagellum*
*Micrurus f. fulvius*
*Natrix c. cyclopion*
*Natrix e. flavigaster*
*Natrix kirtlandii*
*Natrix rhombifera*
*Natrix septemvittata*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Pituophis melanoleucas*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Tantilla c. coronata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (14)

*Coluber c. flaviventris*
*Crotalus adamanteus*
(Garman 1894; Funkhouser 1925)
*Diadophis p. arnyi*
*Natrix s. confluens*
*Natrix s. fasciata*
(Garman; Funkhouser 1925; Jan 1864-5)
*Natrix s. pleuralis*
(Clay 1938)
*Opheodrys v. blanchardi*
*Opheodrys v. vernalis*
*Pituophis c. sayi*
*Sistrurus c. catenatus*
*Thamnophis radix butleri*
Garman 1890; Funkhouser 1925)
*Thamnophis s. proximus*
(Funkhouser 1925)
*Tropidoclonion lineatum*

**Louisiana**

I. *Accredited* (50)

*Abastor erythrogrammus*
*Agkistrodon c. contortrix*
*Agkistrodon p. leucostoma*
*Carphophis a. vermis*
*Cemophora coccinea*
*Coluber c. anthicus*
*Coluber c. constrictor*
*Coluber c. flaviventris*
*Crotalus adamanteus*

*Crotalus h. atricaudatus*
*Diadophis p. stictogenys*
*Drymarchon c. couperi*
*Elaphe guttata*
*Elaphe o. confinis*
*Elaphe o. obsoleta*
*Farancia a. reinwardtii*
*Haldea striatula*
*Haldea v. elegans*
*Heterodon platyrhinos*
*Heterodon simus*
*Lampropeltis calligaster*
*Lampropeltis d. amaura*
*Lampropeltis d. doliata*
*Lampropeltis g. holbrooki*
*Masticophis f. flagellum*
*Micrurus f. fulvius*
*Micrurus f. tenere*
*Natrix clarki*
*Natrix c. cyclopion*
*Natrix e. flavigaster*
*Natrix e. transversa*
*Natrix grahami*
*Natrix rhombifera*
*Natrix rigida*
*Natrix s. confluens*
*Natrix s. fasciata*
*Natrix s. pleuralis*
*Natrix taxispilota*
*Opheodrys aestivus*
*Pituophis m. ruthveni*
*Rhadinea flavilata*
*Sistrurus m. streckeri*
*Storeria d. temporalineata* intergrades
*Storeria d. texana*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Tantilla c. coronata*
*Tantilla gracilis gracilis*
*Thamnophis s. sirtalis*
*Thamnophis s. proximus*

II. Problematic (13)

*Carphophis a. helenae* (Conant and Bridges 1939 Gen)
*Crotalus atrox*
*Dimades plicatis* (Gray 1948 New Orleans)
*Coluber spiloides* (Beyer 1897; Jan 1863; Cope 1900)
*Elaphe o. lindheimeri* (*obsoleta, confinis* and (*lindheimeri* in this state and several others)
*Lampropeltis d. syspila* (Beyer 1897)
*Natrix s. sipedon* (Beyer 1897)
*Pituophis c. sayi*
*Sistrurus m. barbouri*
*Thamnophis s. sauritus*
*Thamnophis s. sackeni*

## Maine

I. Accredited (10)

*Carphophis a. amoena* (Babcock 1929)
*Coluber c. constrictor*
*Diadophis p. edwardsii*
*Lampropeltis d. triangulum*
*Natrix s. sipedon*
*Opheodrys v. vernalis*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (3)

*Carphophis a. amoenus* (Henshaw 1904; Verrill 1863; Allen 1868; Lowe 1928; Norton 1929)
*Crotalus h. horridus* (Williamson 1832; Adams 1873; Lowe 1928; Norton 1929)
*Opheodrys aestivus* (Verrill 1863)
*Thamnophis s. parietalis* (Verrill 1863)

## Maryland

I. Accredited (26)

*Abastor erythrogrammus*
*Agkistrodon c. mokeson*
*Carphophis a. amoena*
*Cemophora coccinea*
*Coluber c. constrictor*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Diadophis p. punctatus*
*Elaphe guttata*
*Elaphe o. obsoleta*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Lampropeltis c. rhombomaculatus*
*Lampropeltis d. temporalis*
*Lampropeltis d. triangulum*
*Lampropeltis g. getulus*
*Natrix e. erythrogaster*
*Natrix septemvittata*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. ventralis*
*Pituophis melanoleucus*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (9)

*Agkistrodon m. austrinus* (McCauley 1936; Gloyd & Conant 1943)
*Crotalus h. atricaudatus*
*Elaphe o. confinis* (Kelly & Robertson 1936)

*Elaphe q. quadrivittata*
(Kelly & Robertson 1936)
*Lampropeltis e. virginiana*
(Blanchard)
*Lampropeltis d. amaura*
(Kelly & Robertson 1936)
*Natrix e. erythrogaster*
(Kelly & Robertson 1936)
*Natrix rigida*
(Kelly, Robertson, Davis 1936)
*Natrix taxispilota*
(Kelly, Robertson, Davis 1936)

**Massachusetts**

I. Accredited (14)

*Agkistrodon d. mokeson*
*Carphophis a. amoena*
*Coluber c. constrictor*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Elaphe o. obsoleta*
*Heterodon platyrhinos*
*Lampropeltis d. triangulum*
*Natrix s. sipedon*
*Opheodrys v. vernalis*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (5)

*Elaphe v. vulpinus*
(Bartlett 1861; Allen 1869; Brown 1902; Henshaw 1904)
*Lampropeltis g. getulus*
(Linsley 1843; Babcock 1920)
*Natrix s. fasciata*
(Jan 1864-5)
*Opheodrys aestivus*
(Babcock 1929)
*Haldea striatulus*
(Smith 1833; Babcock 1920; J. A. Allen 1868)

**Michigan**

I. Accredited (19)

*Coluber c. flaviventris*
*Diadophis p. edwardsii*
*Elaphe o. obsoleta*
*Elaphe v. gloydi*
*Elaphe v. vulpina*
*Heterodon platyrhinos*
*Lampropeltis d. triangulum*
*Natrix e. neglecta*
*Natrix kirtlandii*
*Natrix septemvittata*
*Natrix s. sipedon*
*Opheodrys v. vernalis*
*Sistrurus c. catenatus*
*Storeria d. texana*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis r. butleri*
*Thamnophis s. sirtalis*

II. Problematic (17)

*Agkistrodon mokeson*
(Gibbs, Notestein, Clark 1905)
*Carphophis a. helenae*
(Gibbs 1895; Gibbs, Notestein, Clark 1905; Notestein 1905)
*Crotalus h. horridus*
(Gibbs, Notestein, Clark 1895; Notestein 1906; Gloyd 1940)
*Elaphe guttata*
(Gibbs, Notestein, Clark 1905; Clark 1904)
*Lampropeltis calligaster*
(Smith 1875)
*Lampropeltis g. nigra*
Gibbs, Notestein, Clark 1905)
*Natrix grahami*
(Smith 1879; Gibbs 1895; Notestein 1905; Gibbs, Notestein & Clark 1905)
*Natrix rhombifera* (Gibbs 1895)
(Davis & Rice 1883; Hay 1892; Hunter 1911)
*Natrix s. confluens*
(Stejneger & Barbour 1923; subsequent editions Missouri)
*Natrix s. insularum*
*Opheodrys aestivus* (Smith 1879)
*Pituophis melanoleucus*
(Gibbs, Davis & Rice 1883)
*Pituophis s. sayi*
(Gibbs 1925; Gibbs, Notestein Clark 1905)
*Sistrurus miliarius*
(Smith 1875)
*Thamnophis s. proximus*
(Kirsch 1895; Smith 1879)
*Thamnophis s. parietalis*

## Minnesota

I. Accredited (19)

*Coluber c. flaviventris*
*Crotalus h. horridus*
*Diadophis p. arnyi*
*Diadophis p. edwardsii*
*Elaphe v. vulpina*
*Heterodon platyrhinos*
*Heterodon nasicus*
*Lampropeltis calligaster*
*Lampropeltis d. syspila*
*Lampropeltis d. trianuglum*
*Opheodrys v. blanchardi*
*Opheodrys v. vernalis*
*Pituophis c. sayi*
*Sistrurus c. catenatus*
*Stoneria d. texana*
*Storeria o. occipitomaculata*
*Thamnophis s. parietalis*
*Thamnophis radix haydeni*
*Thamnophis s. proximus*

II. Problematic (9)

*Diadophis p. stictogenys* (Blanchard; Breckenridge 1942)
*Elaphe o. obsoleta*
*Haldea striatula* (Breckenridge 1937)
*Lampropeltis d. syspila*
*Natrix e. flavigaster*
*Natrix septemvittata*
*Natrix s. sipedon*
*Thamnophis r. radix*
*Thamnophis s. proximus* (Ruthven 1908)

## Mississippi

I. Accredited (43)

*Agkistrodon c. contortrix*
*Agkistrodon c. mokeson*
*Agkistrodon p. leucostoma*
*Carphophis a. amoena*
*Carphophis a. helenae*
*Cemophora coccinea*
*Coluber c. constrictor*
*Crotalus adamanteus*
*Crotalus h. atricaudatus*
*Diadophis p. stictogenys*
*Elaphe guttata*
*Elaphe o. confinis*
*Farancia a. reinwardtii*
*Haldea striatula*
*Haldea v. elegans*
*Heterodon platyrhinos*
*Lampropeltis c. calligaster*
*Lampropeltis c. rhombomaculata*
*Lampropeltis d. amaura*
*Lampropeltis doliata*
*Lampropeltis g. holbrooki*
*Masticophis f. flagellum*
*Micrurus f. fulvius*
*Natrix clarkii*
*Natrix c. cyclopion*
*Natrix e. flavigaster*
*Natrix rhombifera*
*Natrix rigida*
*Natrix s. confluens*
*Natrix s. fasciata*
*Natrix s. pleuralis*
*Opheodrys aestivus*
*Sistrurus m. barbouri*
*Sistrurus m. streckeri*
*Storeria d. temporalineata* intergrades
*Storeria d. texana*
*Storeria d. wrightorum*
*Storeria o. obscura* intergrades
*Storeria o. occipitomaculata*
*Tantilla c. coronata*
*Thamnophis s. sirtalis*
*Thamnophis s. proximus*
*Thamnophis s. sackeni*
*Thamnophis s. sauritus*

II. Problematic (13)

*Abastor erythrogrammus* (Yarrow 1882)
*Coluber spiloides* (Cope 1900)
*Diadophis p. punctatus*
*Drymarchon c. couperi*
*Elaps tristis*
*Haldea v. valeriae*
*Heterodon simus* (Higgins 1873)
*Lampropeltis d. syspila*
*Lampropeltis g. nigra*
*Natrix taxispilota*
*Pituophis m. lodingi*
*Pituophis melanoleucus* (Garman 1884)
*Rhadinae flavilata*

## Missouri

I. Accredited (46)

*Agkistrodon c. contortrix*
*Agkistrodon c. mokeson*
*Agkistrodon p. leucostoma*
*Carphophis a. vermis*
*Coluber c. constrictor*
*Coluber c. flaviventris*
*Crotalus h. atricaudatus*
*Crotalus h. horridus*
*Diadophis p. aryni*
*Diadophis p. stictogenys*
*Elaphe e. emoryi*
*Elaphe o. obsoleta*
*Elaphe v. vulpina*
*Farancia a. reinwardtii*
*Haldea striatula*
*Haldea v. elegans*
*Heterodon platyrhinos*
*Heterodon n. nasicus*
*Lampropeltis calligaster*
*Lampropeltis g. holbrooki*
*Lampropeltis d. syspila*
*Masticophis f. flagellum*
*Natrix c. cyclopion*
*Natrix e. flavigaster*
*Natrix e. transversa*
*Natrix grahami*
*Natrix rhombifera*
*Natrix s. confluens*
*Natrix s. pleuralis*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. blanchardi*
*Pituophis c. sayi*

*Sistrurus c. catenatus*
*Sistrurus c. tergeminus*
*Sonora episcopa*
*Storeria d. texana* intergrades
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Tantilla gracilis hallowelli*
*Thamnophis s. sirtalis*
*Thamnophis s. parietalis*
*Thamnophis radix radix*
*Thamnophis r. haydeni*
*Thamnophis s. proximus*
*Tropidoclonion lineatum*

II. Problematic (13)
*Carphophis a. helenae* (Hurter 1893)
*Coluber f. flavigularis* (Jan 1863)
*Coluber spiloides* (Hurter 1911; he and his protege Strecker confused *E. laeta* with *L. calligaster* from Texas to Mo. yet he was probably right about his *E. emoryi*, 1911: 182)
*Crotalus atrox*
*Crotalus v. viridis*
*Elaphe guttata* (Hurter 1911; Evans 1940; Stejneger & Barbour 1943)
*Elaphe o. confinis* (Hurter 1911)
*Elaphe o. lindheimeri*
*Lampropeltis d. gentilis*
*Micrurus f. fulvius* (Hoy 1854; Hurter 1911)
*Natrix sipedon* races (*confluens, pleuralis, sipedon* in Mo.)
*Tantilla coronata*
*Thamnophis s. sirtalis* (*sauritus*)

## Montana

I. Accredited (9)
*Charina bottae*
*Coluber c. flaviventris*
*Coluber c. mormon*
*Crotalus v. viridis*
*Heterodon n. nasicus*
*Lampropeltis d. gentilis*
*Pituophis c. sayi*
*Thamnophis e. vagrans*
*Thamnophis s. parietalis*
*Thamnophis radix haydeni*

II. Problematic (8)
*Crotalus v. lutosus* (Hayden 1875; Coues & Yarrow 1878)
*Heterodon simus* (Cope 1879)
*Lampropeltis g. californiae* (*boylii* (Coues & Yarrow 1878)
*Lampropeltis multistriatus* (Coues and Yarrow 1878)
*Opheodrys v. blanchardi*
*Natrix s. sipedon* (Hayden 1875)
*Pituophis s. affinis* (Allen; Coues & Yarrow 1878)
*Thamnophis s. proximus* (Allen 1874)

## Nebraska

I. Accredited (32)
*Agkistrodon d. mokeson*
*Arizona e. blanchardi*
*Carphophis a. vermis*
*Coluber c. flaviventris*
*Crotalus h. horridus*
*Crotalus v. viridis*
*Diadophis p. arnyi*
*Elaphe e. emoryi*
*Elaphe e. intermontana* intergrades
*Elaphe o. obsoleta*
*Elaphe v. vulpina*
*Heterodon platyrhinos*
*Heterodon n. nasicus*
*Lampropeltis calligaster*
*Lampropeltis d. gentilis*
*Lampropeltis d. syspila*
*Lampropeltis g. holbrooki*
*Masticophis f. testaceus*
*Natrix grahami*
*Natrix s. sipedon*
*Opheodrys v. blanchardi*
*Pituophis c. sayi*
*Sistrurus c. catenatus*
*Sistrurus c. tergeminus*
*Storeria d. texana*
*Storeria o. occipitomaculata*
*Tantilla nigriceps*
*Thamnophis e. vagrans*
*Thamnophis s. parietalis*
*Thamnophis radix haydeni*
*Thamnophis s. proximus*
*Tropidoclonion lineatum*

II. Problematic (12)
*Bascanion t. taeniatum* (Garman 1882)
*Crotalus lecontei* (Cope 1861-62)
*Diadophis p. docilis* (Taylor 1892a)
*Lampropeltis multistriatus* (Kennicott 1860)
*Natrix septemvittata*
*Opheodrys aestivus* (Yarrow 1882)
*Thamnophis s. faireyi*

(Taylor 1892a)
*Thamnophis s. dorsalis*
(Taylor 1892a)
*Thamnophis s. obscura*
(Taylor 1892a)
*Thamnophis s. sirtalis*
(Taylor 1892a)
*Tropidonotus fasciatus*
(Yarrow 1882)

### Nevada

I. Accredited (31)

*Arizona o. eburnata*
*Charina bottae*
*Charina b. utahensis*
*Chionactis o. talpina*
*Coluber c. mormon*
*Crotalus atrox*
*Crotalus cerastes*
*Crotalus m. pyrrhus*
*Crotalus m. stephensi*
*Crotalus scutulatus*
*Crotalus v. lutosus*
*Hypsiglena t. deserticola*
*Lampropeltis g. californae* (*boylii*)
*Lampropeltis pyromelaena*
*Leptotyphlops h. humilis*
*Masticophis f. piceus* (*frenatum*)
*Masticophis t. teaniatus*
*Pituophis c. deserticola*
*Rhinocheilus l. lecontei*
*Rhinocheilus l. clarus*
*Salvadora hexalepis mohavensis*
*Sonora m. linearis*
*Sonora s. isozona*
*Tantilla utahiensis*
*Thamnophis e. biscutatus*
*Thamnophis e. couchi*
*Thamnophis e. elegans*
*Thamnophis e. vagrans*
*Thamnophis s. parietalis*
*Thamnophis s. fitchi*
*Trimorphodon vandenburghi*

II. Problematic (9)

*Coluber piceus*
(Vandenburgh & Slevin 1921a)
*Crotalus v. oreganus*
*Diadophis r. regalis*
*Lampropeltis d. gentilis*
*Leptotyphlops h. utahiensis*
*Sonora s. isozona*
*Sonora s. gloydi*
*Thamnophis eques*
*Trimorphodon lambda*

### New Hampshire

I. Accredited (11)

*Coluber c. constrictor*
*Crotalus t. horridus*
*Diadophis p. edwardsii*
*Heterodon platyrhinos*
*Lampropeltis t. triangulum*
*Natrix s. sipedon*
*Opheodrys v. vernalis*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (4)

*Agkistrodon c. mokeson*
(Amaral 1927d)
*Carphophis a. amoenus*
(Holbrook 1842; Henshaw 1904)
*Elaphe o. obsoleta*
*Thamnophis s. pallidula*
(Allen 1899 also Me., N. Y.)

### New Jersey

I. Accredited (24)

*Agkistrodon c. mokeson*
*Carphophis a. amoena*
*Cemophora coccinea*
*Coluber c. constrictor*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Diadophis p. punctatus*
*Elaphe guttata*
*Elaphe o. obsoleta*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Lampropeltis d. temporalis*
*Lampropeltis d. triangulum*
*Lampropeltis g. getulus*
*Natrix kirtlandii*
*Natrix septemvittata*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. vernalis*
*Pituophis melanoleucus*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (6)

*Crotalus h. atricaudatus*
*Elaphe o. confinis*
(Hallowell 1857); Stone 1906)
*Elaphe vulpina*
(Nelson 1890)
*Natrix e. erythrogaster*
*Natrix kirtlandii*
*Natrix rhombifera*
(Jan 1863, 1864-65)

## New Mexico

I. Accredited (50)

*Arizona e. blanchardi*
*Arizona elegans elegans*
*Arizona e. occidentalis*
*Arizona e. philipi*
*Coluber c. flaviventris*
*Crotalus atrox*
*Crotalus l. klauberi*
*Crotalus m. molossus*
*Crotalus scutulatus*
*Crotalus v. cerberus*
*Crotalus v. viridis*
*Diadophis r. regalis*
*Elaphe e. emoryi*
*Gyalopion canum*
*Heterodon n. kennerlyi*
*Heterodon n. nasicus*
*Hypsiglena t. ochorhynchus*
*Hypsiglena t. texana*
*Lampropeltis d. gentilis*
*Lampropeltis g. splendidus*
*Lampropeltis pyromelana*
*Leptotyphlops d. dissectus*
*Masticophis bilineatus*
*Masticophis f. lineatulus*
*Masticophis f. piceus (frenatus)*
*Masticophis f. testaceus*
*Masticophis t. taeniatus*
*Micruroides euryxanthus*
*Natrix e. transversa*
*Opheodrys aestivus*
*Opheodrys v. blanchardi*
*Pituophis c. affinis*
*Pituophis c. sayi*
*Rhinocheilus l. tessellatus*
*Salvadora g. grahamiae*
*Salvadora h. deserticola*
*Salvadora h. hexalepis*
*Sistrurus c. tergeminus*
*Sonora episcopa*
*Sonora s. blanchardi*
*Storeria dekayi texana*
*Tantilla atriceps*
*Tantilla nigriceps*
*Thamnophis eques cyrtopsis*
*Thamnophis e. megalops*
*Thamnophis e. vagrans*
*Thamnophis marcianus nigrolateris*
*Thamnophis s. parietalis*
*Thamnophis r. haydeni*
*Thamnophis rufipunctatus*
*Thamnophis s. proximus*

II. Problematic (28)

*Crotalus cerastes* (Yarrow 1882)
*Crotalus c. pulverulentus* (Cope 1884)
*Crotalus l. lepidus*
*Crotalus t. pricei* (Noguchi 1909; Vandenburgh 1924b; Klauber 1934)
*Crotalus v. nuntius*
*Drymarchon c. melanurus* (Bailey 1928)
*Elaphe bairdi*
*Elaphe e. intermontana*
*Elaphe subocularis*
*Elaps tristis* (Yarrow 1882)
*Lampropeltis p. celaenops* (Stejneger 1903, etc.)
*Lampropeltis t. amaura* (Bailey 1913)
*Leptodeira septemtrionalis* (Noguchi 1909)
*Leptotyphlops dulcis*
*Leptotyphlops humilis* (Schmidt 1922)
*Leptotyphlops h. segregus*
*Leptotyphlops myopica* (Taylor 1939)
*Masticophis f. flagellum* (Vandenburgh 1924b)
*Masticophis t. girardi*
*Natrix rhombifera*
*Opheodrys aestivus* (Vandenburgh 1924)
*Pituophis c. deserticola* (Bailey 1913)
*Pituophis s. mexicanus* (Yarrow 1875)
*Phyllorhynchus b. browni* (Medden 1927)
*Salvadora p. hexalepis*
*Sistrurus miliarius* (Yarrow 1882)
*Tantilla planiceps* (Bailey 1913)
*Trimorphodon vilkinsonii*

## New York

I. Accredited (19)

*Agkistrodon d. mokeson*
*Carphophis a. amoena*
*Coluber c. constrictor*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Elaphe o. obsoleta*
*Heterodon platyrhinos*
*Lampropeltis d. triangulum*
*Natrix septemvittata*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. vernalis*
*Pituophis melanoleucus*
*Sistrurus c. catenatus*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis r. brachystoma*
*Thamnophis s. sirtalis*

II. Problematic (5)

*Carphophis a. vermis*
(Wallace 1904)
*Coluber spiloides*
(Boulenger 1894)
*Elaphe vulpina gloydi*
(Conant 1940)
*Lampropeltis g. getulus*
(DeKay 1842; Hough 1852; Engelhardt 1913)
*Thamnophis s. parietalis*
(Weed 1922)

## North Carolina

I. Accredited (46)

*Abastor erythrogrammus*
*Agkistrodon d. contortrix*
*Agkistrodon d. mokeson*
*Agkistrodon p. piscivorus*
*Carphophis a. amoena*
*Cemophora coccinea*
*Coluber c. constrictor*
*Crotalus adamanteus*
*Crotalus h. atricaudatus*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Diadophis p. punctatus*
*Elaphe guttata*
*Elaphe o. confinis*
*Elaphe o. obsoleta*
*Elaphe o. quadrivittata*
*Farancia a. abacura*
*Haldea striatula*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Heterodon simus*
*Lampropeltis c. rhombomaculata*
*Lampropeltis d. doliata*
*Lampropeltis d. temporalis*
*Lampropeltis d. triangulum*
*Lampropeltis g. getulus*
*Masticophis f. flagellum*
*Micrurus f. fulvius*
*Natrix e. erythrogaster*
*Natrix septemvittata*
*Natrix s. fasciata*
*Natrix s. pleuralis*
*Natrix s. sipedon*
*Natrix taxispilota*
*Opheodrys aestivus*
*Opheodrys v. vernalis*
*Pituophis m. melanoleucus*
*Rhadinea flavilata*
*Seminatrix pygaea paludis*
*Sistrurus m. miliarius*
*Storeria d. dekayi*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Tantilla coronata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (9)

*Coluber spiloides*
(Cope 1900)
*Elaphe o. parallela*
*Lampropeltis e. virginiana*
(Blanchard 1921; Brimley)
*Natrix s. engelsi*
*Drymarchon c. couperi*
(Brimley 1926)
*Lampropeltis g. stictoseps*
*Natrix cyclopion*
(Jan 1864-5)
*Natrix rigida*
(Jan 1864-5)
*Pituophis m. mugitus*

## North Dakota

I. Accredited (9)

*Coluber c. flaviventris*
*Crotalus v. viridis*
*Heterodon n. nasicus*
*Heterodon platyrhinos*
*Opheodrys v. blanchardi*
*Pituophis c. sayi*
*Storeria o. occipitomaculata*
*Thamnophis s. parietalis*
*Thamnophis radix haydeni*

II. Problematic (6)

*Elaphe v. vulpina*
*Lampropeltis d. gentilis*
*Thamnophis e. vagrans*
(Coues 1875)
*Thamnophis s. ordinatus*
*Thamnophis s. proximus*
(Allen 1874)
*Tropidoclonion lineatum*

## Ohio

I. Accredited (27)

*Agkistrodon d. mokeson*
*Carphophis a. helenae*
*Coluber c. constrictor*
*Coluber c. flaviventris*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Elaphe o. obsoleta*
*Elaphe v. gloydi*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Lampropeltis d. triangulum*
*Lampropeltis g. nigra*
*Natrix e. neglecta*
*Natrix kirtlandii*
*Natrix septemvittata*
*Natrix s. insularum*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. blanchardi*
*Opheodrys v. vernalis*
*Sistrurus c. catenatus*
*Storeria d. dekayi*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis r. butleri*
*Thamnophis s. sirtalis*

II. Problematic (15)

*Agkistrodon p. leucostoma* (Hurter 1911)
*Cemophora coccinea* (Conant 1938)
*Diadophis p, arnyi* (Cope; Morse 1904; Conant 1938)
*Haldea v. elegans* (Morse 1904)
*Lampropeltis calligaster* (Smith 1882; Morse 1904; Conant 1938)
*Lampropeltis d. syspila* (Smith 1882; Hughes; Morse 1904; Cope 1900)
*Natrix c. cyclopion* (Conant 1938)
*Natrix rhombifera* (Smith 1882; Conant 1938)
*Natrix s. fasciata* (Kirtland 1838; Morse 1904; Conant 1938)
*Pituophis melanoleucus* (Smith 1882; Garman 1884; Bumpus 1885; Morse 1904; Davis & Rice 1883)
*Pituophis c. sayi* (Notestein 1905)
*Thamnophis r. brachystoma*
*Thamnophis s. proximus* (Smith 1882)
*Tropidoclonion lineatum* (Yarrow 1882; Stejneger 1891; Cope 1900; Morse 1904; Conant 1938; Dunn 1932)

## Oklahoma

I. Accredited (66)

*Agkistrodon d. laticinctus*
*Agkistrodon d. mokeson*
*Agkistrodon p. leucostoma*
*Arizona e. blanchardi*
*Arizona e. elegans*
*Carphophis a. vermis*
*Cemophora coccinea*
*Coluber c. flaviventris*
*Crotalus atrox*
*Crotalus h. horridus*
*Crotalus v. viridis*
*Diadophis p. arnyi*
*Elaphe e. emoryi*
*Elaphe o. confinis*
*Elaphe o. lindheimeri*
*Elaphe o. obsoleta*
*Farancia a. reinwardtii*
*Haldea striatula*
*Haldea v. elegans*
*Heterodon contortrix*
*Heterodon nasicus*
*Hypsiglena t. ochrorhynchus*
*Lampropeltis calligaster*
*Lampropeltis d. amaura*
*Lampropeltis d. gentilis*
*Lampropeltis d. syspila*
*Lampropeltis g. holbrooki*
*Lampropeltis g. splendida*
*Leptotyphlops d. dulcis*
*Leptotyphlops d. dissectus*
*Masticophis f. flagellum*
*Masticophis f. testaceus*
*Micrurus f. fulvius*
*Natrix e. flavigaster*
*Natrix e. transversa*
*Natrix grahami*
*Natrix rhombifera*
*Natrix rigida*
*Natrix septemvittata*
*Natrix s. confluens*
*Natrix s. fasciata*
*Natrix s. sipedon*
*Opheodrys asetivus*
*Opheodrys v. blanchardi*
*Pituophis c. sayi*
*Rhinocheilus l. tessellatus*
*Sistrurus c. catenatus*
*Sistrurus c. tergeminus*
*Sistrurus m. streckeri*
*Sonora episcopa*
*Storeria d. texana*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Tantilla atriceps*
*Tantilla gracilis gracilis*
*Tantilla gracilis hallowelli*
*Tantilla n. fumiceps*
*Tantilla nigriceps*
*Thamnophis e. vagrans*
*Thamnophis marcianus*
*Thamnophis s. sirtalis*
*Thamnophis s. parietalis*
*Thamnophis radix haydeni*
*Thamnophis s. proximus*
*Tropidoclonion lineatum*

II. Problematic (10)

*Amphiardis inornatus* (Schmidt 1919)
*Coluber spiloides* (Cope 1894; Hurter 1911)
*Crotalus h. atricaudatus*
*Diadophis docilis* (Cope 1894; Stone 1903)
*Diadophis p. stictogenys*
*Coluber t. taeniatus*
*Micrurus f. fulvius* (Ortenburger 1927)
*Natrix c. cyclopion*
*Natrix s. fasciata*
*Opheodrys v. blanchardi* (Ortenburger 1927c)

## Oregon

I. Accredited (24)

*Charina bottae*
*Charina b. utahensis*
*Coluber c. mormon*
*Contia tenuis*
*Crotalus v. lutosus*
*Crotalus v. oreganus*
*Diadophis a. occidentalis*
*Diadophis a. pulchellus*
*Hypsiglena t. ochrorhynchus*

*Lampropeltis g. californiae (boylii)*
*Lampropeltis z. multicincta*
*Lampropeltis z. zonata*
*Masticophis t. taeniatus*
*Pituophis c. catenifer*
*Pituophis c. deserticola (Pituophis c. heermanni)*
*Sonora s. isozona*
*Thamnophis e. biscutatus*
*Thamnophis e. elegans*
*Thamnophis e. hydrophila*
*Thamnophis e. vagrans*
*Thamnophis ordinoides*
*Thamnophis sirtalis concinnus*
*Thamnophis s. fitchi*

II. Problematic (8)
*Coluber lateralis* (Gordon 1939)
*Diadophis a. pulchellus* (Cope 1884)
*Eutaenia leptocephala* (Cope 1884; Garman 1884; Brown 1903)
*Rhinocheilus l. lecontei* (Gordon 1939)
*Thamnophis o. atratus* (Gordon 1939; Fitch 1940; Anderson and Slater 1941)
*Thamnophis radix* (Davis & Rice 1883)
*Thamnophis s. infernalis* (Graf, Jewell & Gordon 1939; Slater 1942)
*Thamnophis s. pickeringii* (Jan 1864-5; Cope 1884; Fitch 1941)

## Pennsylvania

I. Accredited (23)
*Agkistrodon d. mokeson*
*Carphophis a. amoena*
*Coluber c. constrictor*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Elaphe o. obsoleta*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Lampropeltis d. triangulum*
*Lampropeltis g. getulus*
*Natrix e. flavigaster*
*Natrix kirtlandii*
*Natrix septemvittata*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Opheodrys v. vernalis*
*Sistrurus c. catenatus*
*Storeria d. dekayi*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Thamnophis sauritus*
*Thamnophis r. brachystoma*
*Thamnophis s. sirtalis*

II. Problematic (11)
*Carphophis a. helenae*
*Elaphe o. confinis* (Stone 1906)
*Elaphe vulpinus* (Jordan;! Surface 1906; Roddy 1928)
*Haldea striatula* (Surface 1906; Roddy 1928)
*Lampropeltis e. virginiana*
*Lampropeltis t. temporalis*
*Lampropeltis t. niger* (Surface 1906)
*Lampropeltis g. sayi* (Surface 1906)
*Natrix e. erythrogaster* (Are eastern and western Pa. forms the same or mistakes?)
*Natrix rigida* (Higgins 1873; Cope 1900; Surface 1906)

## Rhode Island

I. Accredited (12)
*Carphophis a. amoena*
*Coluber c. constrictor*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Heterodon platyrhinos*
*Lampropeltis d. triangulum*
*Natrix s. sipedon*
*Opheodrys v. vernalis*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (6)
*Agkistrodon c. mokeson* (Drowne 1905; Bumpus 1885)
*Elaphe o. obsoleta* (Drowne 1905)
*Elaphe vulpina* (Drowne 1905)
*Haldea striatula* (Drowne 1905)
*Lampropeltis g. getulus* (Drowne 1905)
*Opheodrys v. vernalis* (Drowne 1905)

## South Carolina

I. Accredited (48)
*Abastor erythrogrammus*
*Agkistrodon c. contortrix*
*Agkistrodon d. mokeson*
*Agkistrodon p. piscivorus*
*Carphophis a. amoena*
*Cemophora coccinea*

*Coluber c. constrictor*
*Crotalus adamanteus*
*Crotalus h. atricaudatus*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Diadophis p. punctatus*
*Drymarchon c. couperi*
*Elaphe guttata*
*Elaphe o. confinis*
*Elaphe o. obsoleta*
*Elaphe o. quadrivittata*
*Haldea striatula*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Heterodon simus*
*Lampropeltis c. rhombomaculata*
*Lampropeltis d. doliata*
*Lampropeltis d. triangulum*
*Lampropeltis g. getulus*
*Masticophis f. flagellum*
*Micrurus f. fulvius*
*Natrix c. floridana*
*Natrix e. erythrogaster*
*Natrix rigida*
*Natrix septemvittata*
*Natrix s. fasciata*
*Natrix s. pleuralis*
*Natrix taxispilota*
*Opheodrys aestivus*
*Pituophis melanoleucus*
*Pituophis m. mugitus*
*Rhadinea flavilata*
*Seminatrix pygaea paludis*
*Sistrurus m. barbouri*
*Sistrurus m. miliarius*
*Storeria d. dekayi*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Storeria o. obscura* intergrades
*Tantilla coronata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (8)

*Ablabes occipitalis* (Gunther 1858; Blanchard and Gloyd 1940)
*Coluber molossus* (Harlan 1827)
*Coluber spiloides* (Cope 1900)
*Crotalus d. melanurus* (Jan 1863)
*Lampropeltis t. syspila* (Pickens 1927)
*Natrix cyclopion* (Jan 1864-5)
*Natrix sipedon* (Pickens 1927)
*Opheodrys v. vernalis* (Grobman 1941)
*Sistrurus c. catenatus* (Jan 1863)

### South Dakota

I. Accredited (17)

*Coluber c. flaviventris*
*Crotalus v. viridis*
*Diadophis p. arnyi*
*Elaphe v. vulpina*
*Heterodon platyrhinos*
*Heterodon nasicus*
*Lampropeltis d. gentilis*
*Lampropeltis d. syspila*
*Opheodrys v. blanchardi*
*Pituophis c. sayi*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Thamnophis e. vagrans*
*Thamnophis s. parietalis*
*Thamnophis radix haydeni*
*Thamnophis s. proximus*
*Tropidoclonion lineatum*

II. Problematic (4)

*Crotalus h. horridus* (Reagen 1908)
*Lampropeltis t. triangulum* (Over 1923)
*Natrix s. sipedon*
*Sistrurus c. catenatus* (Reagen 1908)

### Tennessee

I. Accredited (45)

*Agkistrodon d. contortrix*
*Agkistrodon d. mokeson*
*Agkistrodon p. leucostoma*
*Carphophis a. amoena*
*Carphophis a. helenae*
*Cemophora coccinea*
*Coluber c. constrictor*
*Crotalus h. atricaudatus*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Diadophis p. stictogenys*
*Elaphe guttata*
*Elaphe o. confinis*
*Elaphe o. obsoleta*
*Farancia a. reinwardtii*
*Haldea striatula*
*Haldea v. elegans*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Lampropeltis c. calligaster*
*Lampropeltis c. rhombomaculata*
*Lampropeltis d. doliata*
*Lampropeltis d. syspila*
*Lampropeltis d. triangulum*
*Lampropeltis g. holbrooki*
*Lampropeltis g. nigra*
*Masticophis f. flagellum*
*Natrix c. cyclopion*
*Natrix e. flavigaster*
*Natrix e. transversa*
*Natrix rhombifera*
*Natrix septemvittata*
*Natrix s. confluens*
*Natrix s. pleuralis*
*Natrix s. sipedon*
*Opheodrys aestivus*
*Pituophis m. melanoleucus*
*Pituophis m. mugitus*
*Sistrurus m. streckeri*
*Storeria d. dekayi*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Tantilla c. coronata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (15)

*Abastor erythrogrammus* (Rhoads 1895)
*Agkistrodon atrofuscus* (Troost; Higgins 1873); Rhoads 1895)
*Diadophis p. punctatus* (Troost; Jan 1863; Rhoads 1895)
*Elaphe quadrivittata* (Troost 1844)
*Haldea striatula* (Rhoads 1895)
*Heterodon simus* (Rhoads 1895)
*Lampropeltis d. amaura*
*Micrurus f. fulvius*
*Natrix grahami* (Rhoads 1895)
*Natrix taxispilota* (Rhoads 1895)
*Opheodrys v. vernalis* (Rhoads 1895)
*Pituophis c. sayi* (Rhoads 1895)
*Sistrurus c. catenatus* (Troost; Rhoads 1895)
*Thamnophis radix* (Rhoads 1895)
*Tropidoclonion lineatum* (Rhoads 1895; Dunn 1932)

## Texas

I. Accredited (101)

*Agkistrodon c. contortrix*
*Agkistrodon d. laticinctus*
*Agkistrodon d. pictigaster*
*Agkistrodon p. leucostoma*
*Arizona e. elegans*
*Arizona e. blanchardi*
*Arizona e. philipi*
*Carphophis a. vermis*
*Coluber c. anthicus*
*Coluber c. flaviventris*
*Coluber stejnegerianus*
*Coluber t. girardi*
*Coluber t. ruthveni*
*Coluber t. schottii*
*Coluber t. taeniatus*
*Coniophanes imperialis*
*Crotalus atrox*
*Crotalus h. atricaudatus*
*Crotalus h. horridus*
*Crotalus l. klauberi*
*Crotalus l. lepidus*
*Crotalus molossus*
*Crotalus scutulatus*
*Crotalus v. viridis*
*Diadophis p. arnyi*
*Diadophis p. docilis*
*Diadophis p. stictogenys*
*Diadophis r. blanchardi*
*Drymarchon c. erebennus*
*Elaphe bairdi*
*Elaphe e. emoryi*
*Elaphe o. lindheimeri*
*Elaphe subocularis*
*Farancia a. reinwardtii*
*Ficimia streckeri*
*Gyalopion canum*
*Haldea striatula*
*Haldea v. elegans*
*Heterodon platyrhinos*
*Heterodon n. kennerlyi*
*Heterodon n. nasicus*
*Hypsiglena t. texana*
*Lampropeltis alterna*
*Lampropeltis blairi*
*Lampropeltis calligaster*
*Lampropeltis d. amaura*
*Lampropeltis d. annulata*
*Lampropeltis d. gentilis*
*Lampropeltis g. holbrooki*
*Leptodeira annulata septentrionalis*
*Leptotyphlops d. dulcis*
*Leptotyphlops d. dissectus*
*Leptotyphlops p. segregus*
*Masticophis f. flagellum*
*Masticophis f. testaceus*
*Micruroides euryxanthus*
*Micrurus f. tenere*
*Natrix c. cyclopion*
*Natrix e. flavigaster*
*Natrix e. transversa*
*Natrix grahami*
*Natrix harteri*
*Natrix rigida*
*Natrix r. rhombifera*
*Natrix s. clarkii*
*Natrix s. confluens*
*Natrix s. fasciata*
*Opheodrys aestivus*
*Opheodrys v. blanchardi*
*Pituophis c. affinis*
*Pituophis c. sayi*
*Rhadinea flavilata*
*Rhinocheilus l. tessellatus*
*Salvadora g. grahamiae*
*Salvadora h. deserticola*
*Salvadora lineata*
*Sistrurus c. tergeminus*
*Sistrurus m. streckeri*
*Sonora episcopa*
*Sonora s. blanchardi*
*Sonora taylori*
*Storeria d. temporalineata*
*Storeria d. texana*
*Storeria o. occipitomaculata*
*Tantilla atriceps*
*Tantilla gracilis*
*Tantilla n. fumiceps*
*Tantilla nigriceps*
*Thamnophis e. vagrans*
*Thamnophis eques cyrtopsis*
*Thamnophis eques megalops*
*Thamnophis m. marcianus*
*Thamnophis m. nigrolatrealis*
*Thamnophis sirtalis*
*Thamnophis rufipunctatus*
*Thamnophis s. proximus*
*Trimorphodon vilkinsoni*
*Tropidoclonion lineatum*

II. Problematic (27)

*Amphiardis inornatus* (Garman 1882; Strecker 1915; Vandenburgh 1920)
*Ancistrodon p. pugnax* (Hallowell 1857; Baird 1859; Yarrow 1882; Garman 1885; etc.)
*Cemophora coccinea*
*Coluber c. constrictor* (Strecker 1902; 1908c, 1915, 1926)
*Crotalus adamanteus* (Garman 1897; Strecker 1908b; Mitchell 1923)
*Crotalus lucifer* (Garman 1887)
*Crotalus ornatus* (Hallowell 1856)
*Diadophis p. stictogenys* (Cope 1880; Strecker & Williams 1927, 1928)
*Drymarchon c. couperi*
*Elaphe o. confinis*

(Records 1926+)
*Elaphe o. obsoleta*
(Garman 1884; Cope 1889; Bailey 1905; Strecker 1926d; Strecker & Williams 1928)
*Elaphis rhinomegas*
(Jan 1863)
*Elaps tristis*
(Yarrow 1882)
*Leptotyphlops myopicus*
*Natrix kirtlandi*
(Jan 1864-5)
*Natrix septemvittata*
(Garman 1884
Strecker 1915 Bateman 1897; Boulenger 1893
*Natrix rigida*
(Strecker & Williams 1928)
*Nerodia woodhousii*
(Jan 1864-5)
*Opthalmidion longissimum*
(Garman 1884)
*Pituophis d. deppei*
(Stull 1940)
*Sistrurus c. consors*
(Barid 1859; Mitchell 1903; Bailey 1905; Strecker 1908+)
*Sistrurus c. catenatus*
(Garman 1892)
*Storeria d. wrightorum*
*Thamnophis m. megalops*
(Burt & Burt 1929)
*Thamnophis radix*
(Cope; Ruthven; Strecker 1915)
*Thamnophis s. parietalis*
(several)
*Tropidonotus hammondi*
(Jan 1864-5)
*Tropidonotus obliquis*
(Garman)

## Utah

I. Accredited (31)

*Azizona e. eburnata*
*Charina bottae utahensis*
*Coluber c. mormon*
*Crotalus cerastes*
*Crotalus scutulatus*
*Crotalus v. decolor*
*Crotalus v. lutosus*
*Crotalus v. viridis*
*Diadophis r. regalis*
*Elaphe e. intermontana*
*Herotodon nasicus*
*Hypsiglena t. deserticola*
*Hypsiglena t. loreala*
*Lampropeltis g. californiae*
(*Boylii*)
*Lampropeltis d. gentilis*
*Lampropeltis pyromelana*
*Leptotyphlops h. utahiensis*
*Masticophis f. piceus*
(*frenatus*)
*Masticophis t. taeniatus*
*Micruroides euryxanthus*
*Opheodrys v. blanchardi*
*Pituophis c. deserticola*
*Rhinocheilus l. lecontei*
*Salvadora hexalepis mohavensis*
*Sonora s. gloydi*
*Sonora s. isozona*
*Tantilla utahiensis*
*Thamnophis e. vagrans*
*Thamnophis eques cyrtopsis*
*Thamnophis s. parietalis*
*Trimorphodon lambda*

II. Problematic (9)

*Coluber c. flaviventris*
(Cope 1872; Tanner 1935)
*Coluber piceus*
(Tanner 1927, 1927a; Woodbury 1928)
*Crotalus lecontei*
(Cope 1861-62)
*Crotalus oreganus*
(Tanner 1927)
*Natrix valida*
(Cope 1862)
*Pituophis c. stejnegeri*
(Vandenburgh; Tanner 1927a; Woodbury 1928)
*Pituophis c. sayi*
*Sonora m. miniata*
*Sistrurus c. catenatus*
(Hay 1892; Gloyd 1940)
*Sonora occipitalis*
(Stickel 1938)

## Vermont

I. Accredited (10)

*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Elaphe o. obsoleta*
(Trapido, Baarslag)
*Lampropeltis d. triangulum*
*Natrix s. sipedon*
*Opheodrys v. vernalis*
*Storeria d. dekayi*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (4)

*Agkistrodon c. mokeson*
*Carphophis a. amoena*
*Coluber c. constrictor*
(Thompson 1842; Henshaw 1904)
*Pituophis melanoleucus*

## Virginia

I. Accredited (35)

*Abastor erythrogrammus*
*Agkistrodon d. contortrix*
*Agkistrodon d. mokeson*
*Agkistrodon p. piscivorus*
*Carphophis a. amoena*
*Cemophora coccinea*
*Coluber c. constrictor*
*Crotalus h. atricaudatus*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Diadophis p. punctatus*
*Elaphe guttata*
*Elaphe o. obsoleta*
*Farancia a. abacura*
*Haldea striatula*

*Haldea v. valeriae*
*Heterodon platyrhinos*
*Lampropeltis c. rhombomaculata*
*Lampropeltis d. temporalis*
*Lampropeltis d. triangulum*
*Lampropeltis g. getulus*
*Natrix e. erythrogaster*
*Natrix rigida*
*Natrix septemvittata*
*Natrix s. sipedon*
*Natrix taxispilota*
*Opheodrys aestivus*
*Opheodrys v. vernalis*
*Pituophis melanoleucas*
*Storeria d. dekayi*
*Storeria d. wrightorum*
*Storeria o. ocicpitomaculata*
*Tantilla coronata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (6)

*Cemophora coccinea*
*Crotalus adamanteus* (Brady 1927)
*Elaphe o. confinis* (Hurter 1911)
*Lampropeltis e. virginiana*
*Lampropeltis t. temporalis*

## Washington

I. Accredited (17)

*Charina bottae*
*Charina b. utahensis*
*Coluber c. mormon*
*Contia tenuis*
*Crotalus v. oreganus*
*Diadophis a. occidentalis*
*Hypsiglena t. deserticola*
*Lampropeltis z. multicincta*
*Lampropeltis z. zonata*
*Pituophis c. catenifer*
*Pituophis c. deserticola*
*Thamnophis e. nigrescens*
*Thamnophis e. vagrans*
*Thamnophis ordinoides*
*Thamnophis sirtalis concinnus*
*Thamnophis s. pickeringii*
*Thamnophis s. fitchi*

II. Problematic (7)

*Coluber t. taeniatus*
*Coluber c. flaviventris* (Blanchard 1920)
*Eutaenia leptocephala* (Jan 1864-5; Cope 1893; McLain 1899; Brown 1903)
*Pituophis c. heermanni*
*Thamnophis e. biscutatus* (Owen 1940)
*Thamnophis s. parietalis* (Owen 1940)
*Thamnophis s. trilineata* (Cope 1893; Fitch 1941)

## West Virginia

I. Accredited (22)

*Agkistrodon c. mokeson*
*Carphophis a. amoena*
*Carphophis a. helenae*
*Coluber c. constrictor*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Elaphe o. obsoleta*
*Haldea v. valeriae*
*Heterodon platyrhinos*
*Lampropeltis d. triangulum*
*Lampropeltis g. getulus*
*Lampropeltis g. nigra*
*Natrix e. neglecta*
*Natrix septemvittata*
*Natrix s. sipedon*
*Opheodrys aestivus* (Netting-Grobman 1941)
*Opheodrys v. vernalis*
*Storeria d. dekayi*
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Thamnophis s. sauritus*
*Thamnophis s. sirtalis*

II. Problematic (4)

*Agkistrodon piscivorus* (Hickman 1922)
*Natrix kirtlandii*
*Natrix taxispilota* (Bond 1931)
*Sistrurus c. catenatus*

## Wisconsin

I. Accredited (24)

*Coluber c. flaviventris*
*Crotalus h. horridus*
*Diadophis p. edwardsii*
*Diadophis p. arnyi*
*Elaphe o. obsoleta*
*Elaphe vulpina*
*Heterodon contortrix*
*Lampropeltis calligaster*
*Lampropeltis d. triangulum*
*Natrix kirtlandii*
*Natrix septemvittata*
*Natrix s. sipedon*
*Opheodrys v. blanchardi*
*Opheodrys v. vernalis*
*Pituophis c. sayi*
*Sistrurus c. catenatus*
*Storeria d. texana* intergrades
*Storeria d. wrightorum*
*Storeria o. occipitomaculata*
*Thamnophis s. sirtalis*
*Thamnophis s. parietalis*
*Thamnophis radix radix*
*Thamnophis s. proximus*

II. Problematic (10)

*Coluber c. constrictor* (Pope & Dickinson 1928)
*Crotalus atrox* (Pope 1928)
*Heterodon simus* (Hoy 1883; Higley 1889)
*Natrix e. neglecta*
*Natrix grahami* (Higley; Pope & Dickinson 1928)
*Lampropeltis g. holbrooki* (Davis & Rice 1883; Hoy; H. Garman 1892; Blanchard 1921)
*Natrix rhombifera* (Higley 1889; Pope & Dickinson 1928)
*Opheodrys aestivus* (Pope & Dickinson 1928)
*Thamnophis r. butleri*
*Thamnophis s. sauritus* (Higley 1889; Pope & Dickinson 1928)

## Wyoming

I. Accredited (14)

*Charina bottae utahensis*
*Coluber c. flaviventris*
*Crotalus v. decolor*
*Crotalus v. viridis*
*Heterodon nasicus*
*Lampropeltis d. gentilis*
*Lampropeltis g. holbrooki*
*Masticophis t. taeniatus*
*Opheodrys v. blanchardi*
*Pituophis c. deserticola*
*Pituophis c. sayi*
*Thamnophis e. vagrans*
*Thamnophis s. parietalis*
*Thamnophis radix haydeni*

II. Problematic (9)

*Diadophis*
*Elaphe emoryi*
*Hypsiglena t. deserticola*
*Hypsiglena t. loreala*
*Lampropeltis calligaster*
*Natrix s. sipedon*
*Pituophis c. affinis* (Cary 1917)
*Sistrurus c. catenatus* (Hayden 1875)
*Thamnophis s. proximus*

## Mexico

1945 Smith, H. M. and E. H. Taylor. An Annotated Checklist and Key to the Snakes of Mexico. Bull. U. S. Nat. Mus. No. 187 pp. IV, 239.

## Lower California

I. Accredited (74)

*Arizona e. eburnata*
*Arizona e. occidentalis*
*Chilomeniscus cinctus*
*Chilomeniscus punctatissimus*
*Chilomeniscus stramineus*
*Chilmeniscus s. esterensis*
*Chionactis o. annulata*
*Crotalus atrox*
*Crotalus cerastes laterorepens*
*Crotalus enyo*
*Crotalus exsul*
*Crotalus lucasensis*
*Crotalus m. mitchelli*
*Crotalus m. pyrrhus*
*Crotalus molossus*
*Crotalus m. muertensis*
*Crotalus ruber*
*Crotalus tortugensis*
*Crotalus v. helleri*
*Diadophis a. anthonyi*
*Diadophis a. similis*
*Elaphe rosaliae*
*Hypsiglena t. klauberi*
*Hypsiglena t. ochrorhynchus*
*Hypsiglena t. slevini*
*Hypsiglena t. tortugensis*
*Lampropelits catalinensis*
*Lampropeltis g. californiae (boylii)*
*Lampropeltis g. californiae*
*Lampropeltis g. conjuncta*
*Lampropeltis g. nitida*
*Lampropeltis g. yumensis*
*Lampropeltis z. agalma*
*Lampropeltis z. herrerae*
*Lampropeltis z. zonata*
*Leptotyphlops h. cahuilae*
*Leptotyphlops h. humilis*
*Leptotyphlops h. slevini*
*Lichanura r. gracia*
*Lichanura r. roseofusca*
*Lichanura trivirgata*
*Masticophis anthonyi*
*Masticophis aurigulus*
*Masticophis barbouri*
*Masticophis f. piceus (frenatus)*
*Masticophis f. piceus (piceus)*
*Masticophis lateralis*
*Micruroides euryxanthus*
*Natrix valida celaeno*
*Pelamydrus platurus*
*Phyllorhynchus d. decurtatus*
*Phyllorhynchus d. perkinsi*
*Pituophis c. annectens*
*Pituophis c. bimaris*
*Pituophis c. coronalis*
*Pituophis c. fuliginatus*
*Pituophis c. insulanus*
*Pituophis d. vertebralis*
*Rhinocheilus l. lecontei*
*Salvadora h. hexalepis*
*Salvadora h. klauberi*
*Salvadora h. virgultea*
*Sonora bancroftae*
*Sonora mosaueri*
*Sonora s. linearis*
*Sonora s. isozona*
*Tantilla eiseni*
*Tantilla e. transmontana*
*Tantilla planiceps*
*Thamnophis digueti*
*Thamnophis e. hammondi*
*Thamnophis e. hueyi*
*Thamnophis e. megalops*
*Thamnophis lyrophanes*

II. Problematic (11)

*Coluber c. flaviventris* (Nelson 1922)
*Crotalus a. elegans* (Schmidt 1922)
*Crotalus goldmani* (Schmidt 1922)
*Crotalus tigris* Mocquard 1899)
*Drymarchon c. melanurus* (Vandenburgh & Slevin 1914)
*Hypsiglena chlorophaea* (Cope 1860; Mocquard 1899)
*Pituophis c. deserticola*
*Rhinocheilus l. clarus*
*Thamnophis e. vagrans* (Vandenburgh & Slevin 1921c; Schmidt 1922)
*Thamnophis eques* (Xantus-Cope 1866; Vandenburgh 1895a)
*Trimorphodon vandenburghi* (Klauber 1940)

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* In anticipation of the International Zoological Committee's adoption of the wish of the majority of the North American herpetologists we employ *sirtalis* and *sauritus* though we have been of Klauber's position since 1910.

# The Ant Larvae of the Subfamily Ponerinae — Part II[1]

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## Tribe PONERINI Forel
## Genus CENTROMYRMEX Mayr

Neck short and stout. Nine differentiated somites. Body beset with a very large number (about 400) of spine-like tubercles,[2] which are so slender as to simulate body hairs; surface of tubercles beset with several fine denticles; base occasionally bearing two long extremely fine hairs. Body hairs restricted to ventral surface. Antennae large. Ventral notch of labrum wide, deep and sclerotized. Posterior surface of labrum with about 20 sensilla. Mandibles straight; basal half of medial and posterior surfaces roughened with scales (?); on the posterior surface these are arranged in transverse rows; on the medial surface they are imbricated and each scale is produced ventrally into a spinule.

*Centromyrmex feae* Emery.—Plate I, figs. 1-10. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a short stout curved neck; remainder of abdomen stout and subovoidal. Diameter greatest at the sixth abdominal somite; diminishing gradually toward the anterior end. Posterior end rounded. Anus ventral. Nine differentiated somites. Body furnished with numerous (about 370) spine-like tubercles, some of which are mounted on low elevations; tubercles uniformly distributed, slender, acuminate; typically with several fine denticles projecting obliquely from the sides; bases slightly swollen; some tubercles are bifurcate; length of tubercles 0.035-0.23 mm; the smallest tubercles lack denticles and have the basal half swollen and the apical half greatly attenuated; the largest tubercles have each two long (0.09 mm) flexuous and extremely fine hairs arising near the base. No tuber-

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1 Part I appeared in Vol. 48 of this journal, pages 111-144. 1952.

2 We have had some doubts about the appropriateness of the term tubercle. Webster's *Collegiate Dictionary* defines it as "a small knoblike prominence or excrescence, esp. on an animal or plant; a nodule . . . *Med.* A small rounded morbid growth in an organ or in the skin." Thus there is a definite connotation of roundness with which few ponerine tubercles could qualify. Torre-Bueno's *Glossary of Entomology,* however, defines *tubercle* as "a little solid pimple or small button." A pimple is pointed and a button may be knob-like (i.e., rounded). So apparently entomological usage takes care of all types of ponerine protuberances, although it must be stretched somewhat to include the spine-like structures of Centromyrmex. But, in any event, myrmecological usage definitely sanctions the term. Müller (1886) used *Tuberkeln* in German when referring to the rounded protuberances of mature Pachycondyla larvae; the subconical structures on the young were called merely *Erhebungen.* Emery in 1899 used *sporgenze segmentali o tubercoli del tegumento* in Italian when referring to both the rounded and the pointed projections of several genera. In the *Genera Insectorum* (1911) Emery used the French *tubercules.* Wheeler first used *tubercles* in 1900 in "A Study of Some Texan Ponerinae" (his second paper on ants) and he was still using it in 1922.

cles on the midventral surface. Body hairs very few; limited to the ventral surface; 4-6 per somite; simple, flexuous, short (0.06-0.16 mm). Integument spinulose on the ventral surface; spinules exceedingly minute and arranged in short transverse rows. Cranium subhexagonal, broader than long, the dorsal corners rounded; occipital border slightly concave. Head hairs few, rather short (0.07-0.12 mm), simple, slightly curved. Antennae large low rounded convexities, bearing three sensilla each. Labrum broader than long ($1\frac{3}{4}$X); narrowed at base; lateral borders sinuate; strongly bilobed due to a wide and deep median notch in the ventral border; surface of notch heavily sclerotized; the anterior surface of each lobe with a low rounded eminence bearing several large sensilla and a few minute hairs. Posterior surface of labrum densely beset with minute spinules; on the middle half the spinules are arranged in long transverse rows; on the lateral quarters the rows are short, arcuate and oblique; with about 20 sensilla arranged in two irregular rows. Mandibles moderately stout and heavily sclerotized; straight; subtriangular in anterior view; base only slightly dilated; apical tooth short, moderately stout, round-pointed, slightly curved medially and posteriorly; two short rather stout blunt teeth on the inner border; inner and posterior surfaces of basal half roughened with scales (?); on the posterior surface these are arranged in transverse rows; on the inner surface they are imbricated and each scale is produced ventrally into a spinule; anterior surface with longitudinal striae. Maxillae conoidal; spinulose, with the spinules minute and mostly in short arcuate rows, but a few on the anterior surface coarser and isolated; palp a subcylindrical peg with four sensilla on its flattened end—one finger-like, one discoidal and two bearing a spinule each; galea twice as long as palp, finger-like, bearing two apical sensilla. Labium subhemispherical; spinulose, the spinules minute and arranged in long transverse rows on the anterior surface, but elsewhere in short arcuate rows; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are in long transverse rows; palp a subcylindrical peg with four sensilla on its flattened end—one finger-like, two paxilliform and one bearing a spinule; opening of sericteries wide and salient. Hypopharynx densely spinulose, the spinules long, fine and arranged in transverse rows. (Material studied: numerous larvae from Java and Indochina.)

Wheeler, 1936, p. 207: "slender, tuberculate larvae."

*Centromyrmex* sp. (in Bolivia).—Mann, 1934, p. 189: "In the chambers of the ants' home I noticed on the top of each larva the body of a decapitated termite. Near by were little piles of dead termites to provide a second helping."

## Genus ODONTOPONERA Mayr

Integument of body with fine ridges forming a reticulate pattern, the ridges bearing at irregular intervals minute spinules. Tubercles moderately numerous (about 100); subconical; of two types—(1) short, stout and blunt, and (2) long and slender with an expanded base and having at or near the tip 0-3 minute acute projections and/or spinule-bearing sensilla; integument of tubercles with numerous encircling rows of minute spinules; no hairs. Body hairs very few and exceedingly minute. Posterior surface of labrum with

eight or nine sensilla on each half. Mandibles elongate and narrow; not curved posteriorly and only slightly curved medially; base not dilated; basal half of posterior surface with short arcuate ridges arranged in transverse rows; each ridge usually bearing one or two spinules, which are pointed ventrally. Maxillary spinules rather long and slender; galea twice as long as palp.

*Odontoponera transversa* (F. Smith).—Plate I, figs. 11-19. Thorax and first abdominal somite forming a short slender neck which is bent ventrally; neck usually straight; remainder of abdomen voluminous and subelliptical in profile; posterior end rounded, produced ventrally into a post-anal boss. Anus ventral. A peculiar ventrolateral integumentary structure on either side of abdominal somites II-VIII. Eleven differentiated somites. Leg vestiges present. Body furnished with approximately 100 subconical tubercles which are 0.05-0.25 mm long and arranged in irregular rows, one row around the middle of each somite; no tubercles on the ventral surface; shorter tubercles stout and blunt; the longer are quite slender, with an expanded base and have at or near the apex 0-3 minute acute projections and/or spinule-bearing sensilla; integument of tubercles with numerous encircling rows of minute spinules. Body hairs very few and exceedingly minute (about 0.009 mm); widely scattered, mostly on ventral surface. Integument of body with fine ridges forming a reticulate pattern, the ridges bearing at irregular intervals minute spinules. Cranium as long as broad; slightly narrowed ventrally; subtrapezoidal in anterior view but with the occipital angles rounded; integument (except on front and clypeus) beset with exceedingly minute spinules which are uniformly distributed, arranged irregularly and either isolated or in groups of two to four. Head hairs few, short (0.045-0.72 mm), stout; tapering gradually throughout most of their length, then rapidly to the point; the tip may be slightly hooked; constricted near the base. Antennae moderately large, each bearing three sensilla. Labrum twice as broad as long; lateral borders sinuate; bilobed due to a deep median incision in the ventral border; near the ventral border of each lobe there is a low convex prominence on the anterior surface, which bears several sensilla and a few minte hairs; middle half of posterior surface densely spinulose, the spinules minute and mostly arranged in long transverse rows; lateral quarters with a few short scattered arcuate rows of minute spinules; ventral border spinulose; posterior surface with eight or nine sensilla scattered irregularly on each lobe. Mandibles elongate and narrow; nearly straight; heavily sclerotized; base not dilated; not arcuate posteriorly; apical tooth long, slender and curved medially; with two rather stout blunt-pointed subapical teeth on the inner border; posterior surface of basal half with short arcuate ridges arranged in transverse rows; each ridge usually bears one or two spinules which point ventrally. Maxillae with the apex paraboloidal and spinulose, the spinules rather long and slender and arranged in short transverse arcuate rows; palp a subcylindrical peg with several sensilla on its rounded distal end; galea finger-like, with two apical sensilla. Labium prominent; anterior surface densely spinulose, the spinules near the center fine and grouped in short transverse rows, the others coarser and isolated; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in numerous short transverse rows; posterior surface less densely spinulose; palp a subcylindrical peg with several

sensilla on its flat apical end; opening of sericteries wide and salient. Hypopharynx densely spinulose, the spinules slender and in transverse rows. (Material studied: a dozen larvae from the Philippine Islands.)

In younger larvae the neck is longer and more slender and the tubercles are more conspicuous.

### Genus DINOPONERA Roger

Neck short and stout. Leg vestiges conspicuous and tuberculate. Body beset with numerous (160) mammiform tubercles; each with 6-25 short flexuous hairs arranged in an irregular circle near the base; often a second circle nearer the apex. Body hairs very few and exceedingly minute. Integumentary spinules on the tubercles arranged in short arcuate rows which form a reticulate pattern. Head small. Cranium transversely subelliptical in anterior view; a third broader than long; a shallow median longitudinal furrow from the occiput to the level of the antennae. Mandibles strongly arcuate posteriorly but only slightly curved medially, with two apical teeth; only one tooth on the medial border. Maxillae densely furnished with long coarse spinules; palps are subcylindrical pegs, with the end flattened and bearing two sensilla each; galea only a little longer than palp.

*Dinoponera grandis mutica* Emery.—Plate II, figs. 1-8. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a short stout strongly curved neck; remainder of abdomen voluminous and nearly straight, its dorsal profile somewhat curved, ventral serrate and nearly straight; ventral surface somewhat flattened. Thoracic somites separated dorsally by deep intersomitic furrows. Posterior end rounded. Anus ventral. Leg vestiges conspicuous and tuberculate. Thirteen differentiated somites. Body thickly beset with approximately 160 mammiform tubercles distributed (on each half) as follows: prothorax (anterior third)—one small dorsal and two small lateral; prothorax (posterior two-thirds)—a medium-sized double dorsal, a medium-sized double lateral and a very small ventrolateral; mesothorax—a large double dorsal, a large lateral and a very small ventrolateral; metathorax—a large double dorsal, a medium-sized lateral and a small ventrolateral; abdominal somite I—a large double dorsal, a double lateral (upper large, lower small) and a small ventrolateral; II—two large dorsal, two lateral and a small ventrolateral; abdominal somites III-VIII have each a vestigial dorsolateral, three large lateral and a small ventrolateral; IX—three small lateral and one small ventrolateral; X—one large ventrolateral; no tubercles on entire midventral surface or on middorsal surface of abdomen. Hairs on tubercles short (0.03-0.37 mm), simple flexuous; 6-25 on each tubercle; arranged in an irregular circle near the base of each tubercle; often a second circle nearer the apex. Body hairs very few and exceedingly minute (about 0.009 mm). Integument mostly spinulose; spinules exceedingly minute; usually arranged in rows; on the tubercles the rows are short and arcuate and form a reticulate pattern. Head small; cranium transversely subelliptical in anterior view; a third broader than long; occipital border broadly rounded and feebly notched at the middle; a median longitudinal furrow extending from this notch to the level of the antennae. Antennae a pair of low conoidal elevations, each bear-

ing three or four sensilla. No hairs on head. Labrum short and broad; breadth twice the length; narrowed at the base; lateral borders convex; ventral border with a shallow depression; anterior surface with two ventrolateral clusters of sensilla and minute hairs (each cluster on a low rounded convexity) and coarse isolated spinules near the ventral and lateral borders. Middle half of posterior surface densely spinulose, the spinules minute but relatively long and slender and arranged in long transverse rows; lateral to the above area the spinules are very sparse, much shorter and grouped in short arcuate rows; near the lateral borders the spinules are isolated, coarse and larger; lateral and ventral borders with coarse isolated spinules; posterior surface with three sensilla on each end of the depression in the ventral border. Mandibles moderately stout; heavily sclerotized; strongly arcuate posteriorly; with two apical teeth which are round-pointed and slightly curved medially; the single tooth on the inner border is acute and rather short. Maxillae large and lobose; apex densely beset with long coarse spinules; palp a slender subcylinder, with two sensilla on the flat apex; galea finger shaped, scarcely longer than the palp and bearing on its apex one or two sensilla. Labium with its anterior surface densely beset with isolated coarse spinules; palp cylindrical, with two sensilla on its flat apex; opening of sericteries broad. Hypopharynx densely beset with fine spinules in transverse rows. (Material studied: the damaged integument of a single larva about 20 mm long, from Brazil, and a photograph.)

Mann, 1916: "A larva probably immature, in alcohol measures 13 mm. in length. The body is thick and the neck short. All the segments are distinct, with fine, short hairs. The head is glabrous, from above a little broader than long; the mandibles are long and acuminate. The thorax and abdomen are tuberculate, the tubercles very large and prominent, rounded above, each bearing a small sensory papilla at the middle. Each segment has three of these large tubercles laterally, and a smaller, less conspicuous one basally" (p. 409). Plate 7, fig. 55, an "immature (?) larva" in side view.

## Genus DIACAMMA Mayr

Neck long and slender. Body beset with tubercles. Integumentary spinules abundant and conspicuous. Cranium subcircular in anterior view; its integument granular. Labrum short and broad; breadth more than twice the length. Mandibles falciform; distal third long, slender and directed medially; with or without a small tooth on its medial surface; the surface of the stout base is roughened with short arcuate transverse spinulose ridges. Maxillae densely furnished with long coarse spinules; integument of base granular; integument of galea rugose. Anterior surface of labium densely beset with long slender sharp spinules; posterior surface granular.

Wheeler, 1910: "The larvae . . . have prominent, pointed, or rounded tubercles which probably have a protective function" (p. 74). "Larvae furnished with rows of tubercles" (p. 233). On page 234 he mentions a possible function of such tubercles—defending the larvae from one another.

*Diacamma australe* (Fabricius).—Plate II, figs. 9-18. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long slender neck, which is strongly bent ventrally; remainder of abdomen stout, straight and elongate-ellipsoid. Posterior end rounded. Anus ventral. Leg vestiges and vestigial gonopods conspicuous. Thirteen differentiated somites. Spiracles small. Body sparsely beset with approximately 72 tubercles, distributed (on each half) as follows: prothorax—a lateral, ventrolateral and a ventral; mesothorax and metathorax—each with a lateral and a ventrolateral; abdomen I—a small lateral; II—two lateral; III-VII—each with two lateral and one ventrolateral; VIII—a dorsolateral, three lateral and a ventrolateral; IX—a dorsal, a dorsolateral, two lateral and a ventrolateral; X— a terminal. Tubercles paraboloidal; each crowned with a number of minute conoidal papillae, girdled near its middle with a zone of reticulate markings and bearing near its base two small hairs (about 0.06 mm long). No tubercles on ventral surface and only one pair on the dorsal. Near each abdominal spiracle and each ventral tubercle there is a peculiar integumental structure of unknown function. Body hairs very few, limited to ventral surface; simple, slightly curved or flexuous; those on the ventral surface of two sizes—0.06 mm and 0.2 mm. Integument densely spinulose; spinules about 0.013 mm long and arranged in short rows of 2-4; rows transverse, except near the tubercles where they are arranged in concentric circles. Cranium subcircular in anterior view; integument granular with minute (0.005 mm) isolated paraboloidal and conoidal tubercles, except on the gula, where it is thickly beset with larger elliptical elevations. Hairs of head few, simple, short, slightly curved, uniformly scattered; constricted at the base; apex acuminate; length about 0.14 mm (except clypeal 0.06 mm). Antennae with three sensilla each. Labrum short and very broad breadth $2^1/_3$X the length); ventral border concave, finely spinulose and furnished with numerous sensilla; ventral corners rounded; lateral borders sinuate; anterior surface with a few spinules in short arcuate rows near the ventral border; in each ventrolateral area of the anterior surface a low convexity bearing a few minute hairs and several sensilla. Posterior surface of labrum spinulose, the spinules of the middle ⅔ minute and arranged in transverse rows; lateral sixths with coarser isolated spinules; very few scattered sensilla. Mandibles falciform; base broad and stout; distal third long, slender and directed medially, bearing a small sharp tooth on its medial surface and terminating as a long, slender apical tooth; the stout base has its surfaces roughened with short transverse arcuate spinulose ridges. Maxillae paraboloidal; densely spinulose, the spinules long, slender and sharp-pointed; integument of base granular like that of the cranium; palp a slender subcylindrical peg with four sensilla on the apex; galea a longer, rugose, finger-like projection with two sensilla on the tip. Labium subhemispherical; integument of posterior surface granular like that of the cranium; anterior surface densely spinulose, the spinules long, slender and sharp-pointed; palp a rather slender subcylindrical peg, with four apical sensilla, one of which is paraboloidal; opening of sericteries wide and salient, with three conspicuous projections. Hypopharynx densely beset with fine spinules in transverse rows. (Material studied: five larvae from Queensland.)

*Diacamma scalpratum* (F. Smith).—Plate II, figs. 19 and 20. In general, similar to *australe,* but differing in the following particulars: Tubercles twice as numerous (160) and arranged in regular rows, one row around the middle of each somite; no tubercles on midventral surface. Tubercles stout and conoidal, bearing 2-6 simple hairs about 0.1 mm long and (on the apex) a long slender smooth slightly curved spine; base densely spinulose, the spinules minute and arranged in regular encircling rows; length of tubercle (including spine) 0.23-0.45 mm, the largest on the thorax. Body hairs moderately numerous and uniformly distributed; short (length about 0.15 mm); apex acuminate. Integumental spinules much smaller. Integument of cranium roughened with minute papillae, which are isolated or in short rows of three or more; lateral to antennae papillae replaced by spinules; integument of gula like that of frons. Head hairs moderately numerous; rather stout and blunt-pointed; only two on clypeus; length about 0.22 mm. Lateral sixths of posterior labral surface with fine spinules in short arcuate rows. Mandibles longer and less curved medially. Palps and galea longer. (Material studied: four larval integuments from India.)

*Diacamma rugosum viridipurpureum* Emery.—Plate II, figs. 21-24. Fundamentally similar to *scalpratum* but differing in the following characters: Tubercles about half as long; length (including spine) 0.15-0.23 mm; apical half of spine roughened with minute denticles, basal half smooth; hairs 1-3, which are about 0.08 mm long. Body hairs very few, widely scattered, short (0.1-0.16 mm), blunt-pointed, with the tip fuzzy. Integumental spinules in short rows which form a reticulate pattern. Integument of cranium as in *australe,* except that of gula, which has minute spinules in short transverse rows. Head hairs acuminate apically. Mandibles without a medial tooth. Spinules on labium fewer and coarser. (Material studied: two larval integuments from the Philippine Islands.)

The young larva (4 mm long) appears to have more tubercles than the adult, but this is due to the relatively larger size of the tubercles (0.1-0.2 mm long); actually the number is approximately the same. The tubercles have the shape of a tall cone; the spine of the mature tubercle of the next-instar integument appears to form the axis of the cone. Each tubercle bears two hairs but no spinules. Body hairs rather stout and about 0.1 mm long; straight or slightly curved or kinked; apex branched or sometimes fuzzy. Integumental spinules about 50% longer than in the mature larva. The labium has a curious median projection from its anteroventral surface; this process is finger-like and long (0.27 mm) and slender (basal diameter 0.07 mm); the distal third is bent forward at a small but distinct angle (artifact?); surface uniformly spinulose, the spinules minute, long and slender. On either side of this median process (but on a more posterior level) there is a prominent hemispherical boss; its surface is glabrous except for a few basal spinules. Is the median process associated with the sericteries, as Emery (1899, p. 5) maintained? We do not know the answer; but we can detect no apical opening; furthermore the silk duct of the next-instar larva is conspicuous and its opening is between the bosses at some distance posterior to base of the process

and has no apparent connection with the latter. (Material studied: a single specimen from the Philippine Islands; the integument of this young larva contains the integument of the next-instar larva.)

*Diacamma rugosum vagans* (F. Smith).—Generally similar to *r. viridipurpureum*, but differing in these respects: the tubercles are about half as long (0.075-0.15 mm); body and head hairs are shorter; integument granular, but many of the granules bear a spinule. (Material studied: two integuments from the Philippine Islands.)

*Diacamma rugosum geometricum* (F. Smith).—Banks, 1904: "White grubs, which are shaped very much like a long-necked gourd, the head being at the smaller end" (p. 9). Fig. 1c, larva in side view.

Emery, 1899: "Nella forma generale del corpo, le larve . . . rassomigliano piuttosto a quelle della *Ponera stigma:* la parte addominale è poco rigonfiata, e i limiti dei segmenti sono distinti. Sopra ciascuno di essi si trova una serie trasversale, irregolare di tubercoli conici, ineguali che, nelle larve più sviluppate, portano da uno a quattro peli. Nelle piccole larve, i tubercoli sono piccoli, subcilindrici e senza peli; negli stadi intermedi passano per una forma acuminata con pochi peli. Nelle larve giovani di questa specie, il labbro inferiore offre, in avanti, una vistosa sporgenza conica, alquanto curvata in su e relativamente maggiore nelle più piccole larve. Questa sporgenza corrisponde alla papilla mediana o filiera, del margine labiale. Nelle larve maggiori, essa è molto ridotta e poco appariscente. Le mandibole sono foggiate diversamente da quelle della *Ponera* e *Odontomachus*, ed hanno forma arcuata con punta acutissima" (p. 5). (Quoted in part by Wheeler, 1900a, p. 19.) Pl. I, fig. 3: *a*, a large larva, apparently immature; *b*, head of younger larva in side view; *c*, same in anterior view; *d*, head of very young larva in side view; *e*, end of abdomen of same; *f*, tubercles of this larva greatly magnified; *g*, tubercles of medium-sized larva. (Emery's figure *b* is reproduced by Berlese, 1925, Fig. 825C on p. 846; figures *b* and *c* by Escherich, 1906, Fig. 31 = 1917, Fig. 37A.)

Wheeler, 1900a, p. 15 (referring to Emery, 1889): "Mandibles powerfully developed for ant-larvae, the anterior portion of the body long and slender and folded over the abdominal portion, and . . . covered with rows of peculiar tubercles beset with more or less prominent hairs."

## Genus MEGAPONERA Mayr

Elongate and very slender; subcylindrical; slightly curved ventrally; no distinct neck. No tubercles or bosses. Body practicaly naked; with only a very few widely scattered and exceedingly minute hairs. Cranium subtrapezoidal in anterior view; broader than long. Antennae small. No hairs on head. Labrum very short and broad; breadth 3X length; ventral border convex. Mandibles long and falciform; base dilated; apical half very slender, sharp-pointed and strongly curved medially; no medial teeth; inner surface of base with few minute spinules irregularly arranged. Apex of maxillae densely furnished with long slender flexuous spinules. Hypopharynx cordate; finely spinulose ridges forming a reticulate pattern.

*Megaponera foetens* (Fabricius).—Plate I, figs. 20-25. Elongate and very slender; subcylindrical; slightly curved ventrally; no distinct neck; diameter greatest at the seventh abdominal somite, decreasing gradually to the anterior end and more abruptly to the posterior end, which is rounded. Anus ventral. Vestigial legs and gonopods present. Thirteen differentiated somites. Body practically naked; a very few exceedingly minute (0.009 mm long), widely scattered hairs. Integument densely beset with exceedingly minute spinules arranged in transverse rows. Integumental structures of unknown nature and function are located on the ventrolateral surfaces of each somite; on the abdomen such structures are also found in the dorsolateral regions and in the intersegmental furrows. Cranium subtrapezoidal, broader than long; occipital corners broadly rounded. No head hairs. Antennae small, with three sensilla each. Labrum very short; breadth 3X length; lateral borders sinuate; ventral border convex, beset with a few sensilla and numerous fine spinules; on the anterior surface near each ventrolateral corner there is a low convexity which bears several sensilla; middle half of anterior surface spinulose, the spinules minute and arranged in transverse rows, a few sensilla and minute hairs scattered among these spinules; median half of posterior surface thickly beset with long parallel transverse ridges, each bearing a row of exceedingly minute spinules, the lateral quarters with short transverse rows of much longer spinules; a few scattered sensilla on the lateral quarters of the posterior surface. Mandibles long and falciform; base dilated; apical half very slender, sharp-pointed, strongly curved medially; inner surface of base with a few minute spinules irregularly arranged. Maxillae with the apex paraboloidal and densely spinulose, the spinules extremely long, slender and flexuous, those on the apex twice as long as those on the sides; palp a rather stout subcylindrical peg, with five sensilla on the blunt-pointed apex; galea finger-like, with two apical sensilla. Labium with the anterior surface densely spinulose, the spinules mostly coarse and isolated, but near the center smaller and grouped in short transverse rows; palp a subcylindrical peg, with four or five apical sensilla; opening of sericteries wide and salient. Hypopharynx cordate; with finely spinulose ridges forming a reticulate pattern. (Material studied: a dozen larval integuments from the Belgian Congo.)

Wheeler, 1918: "The larva is cylindrical, covered with a very tough, opaque, grayish, hairless skin and furnished with long, falcate mandibles" (p. 299). Fig. 3*A*, nearly adult larva in side view; *B*, head in anterior view (p. 300).

Wheeler and Bailey, 1920: "The transverse ridges [of the trophorhinium] are still represented by a reticulate areolation like that of the general integument, except that the meshes are drawn out transversely" (p. 269). Pl. III, fig. 18, a photomicrograph of some of the mouth parts.

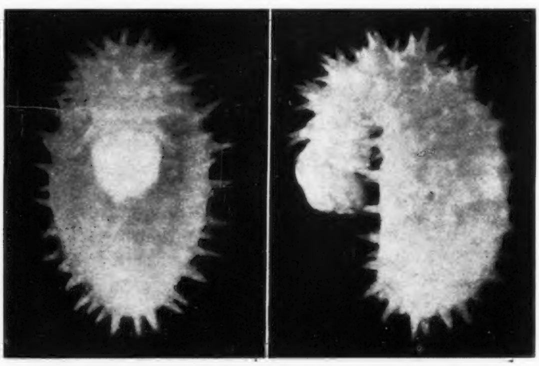
Wheeler, 1922: "The larvae are grayish white, long and subcylindrical, and only slightly curved, with strongly marked segments and with smooth, remarkably tough integument, which is quite hairless in all stages, a condition which I have never observed in any other ant larva. The head is very large, rounded, strongly chitinized, and terminal, with long, acute, falcate, edentate

mandibles, minute vestiges of antennae, and very prominent tactile sensillae on the maxillae and labium. The size of the head and mandibles shows that the larvae are fed on pieces of termites and not with regurgitated liquid food, and the strong integument is evidently an adaptation to exposure to the air and light and to the exigencies of frequent and protracted transportation in the powerful denticulate jaws of the workers. The nudity of the integument indicates that even the very young larvae are carried singly and not in bunches held together by interlocking hairs as in most other species of ants" (pp. 68-69). Fig. 8 on p. 68 = Wheeler, 1918, Fig. 3. On page 56 Wheeler states that the larvae of Megaponera are hairless.

## Genus NEOPONERA Emery

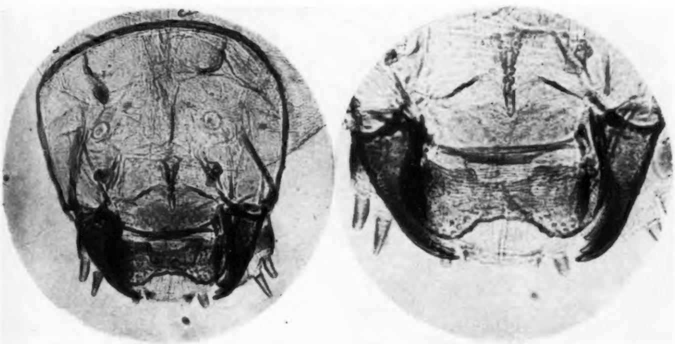
Neck stout and moderately long. Tubercles numerous (140); elongate, slender, subconical; with a few short hairs on the sides; integument roughened with minute spinules in transverse rows; a few apical or subapical sensilla and/or minute hairs. Body hairs minute. Dorsal to each antenna near the occipital border there is a prominent boss bearing a few sensilla and a minute hair. Anterior surface of clypeus roughened with sensilla and minute bosses; rest of cranium spinulose (or partly so). Antennae with a basal disc. Labrum with transverse ridges on the ventral border of the notch; lateral borders of labrum with appressed scales, some of which are produced with spinules. Mandibles narrow and somewhat elongate; some of basal half roughened with minute spinules, which are isolated or in short arcuate rows. Maxillae densely spinulose, the spinules coarse, stiff and sharp-pointed; palp and galea arising close together on a low lateral lobe; galea scarcely longer than palp. Labium densely spinulose, the apical spinules long, coarse, stiff and sharp-pointed.

*Neoponera obscuricornis latreillei* Forel.—Plate III, figs. 15-17 and 19.



Text fig. 1. *Neoponera obscuricornis* Emery.—Left, young larva, ×14; right, side view of same, ×14. (Photographs by E. L. Krause.)

Shaped somewhat like a crook-neck squash; thorax and first two abdominal somites forming a stout moderately long neck, which is strongly bent ventrally; remainder of abdomen moderately stout, nearly straight, subcylindrical; ventral surface flattened and posterior end somewhat flattened, so that their profiles meet at right angles. Anus ventral and surrounded by tubercles. Leg vestiges present. Thirteen differentiated somites. Spiracles mounted on small papillae. Body thickly and conspicuously beset with approximately 140 elongate, slender subconical tubercles which are 0.2-0.5 mm long (longest on the sides) arranged in 12 longitudinal rows and apportioned thus: thoracic somites, 10 each; abdominal somites I-VIII, 12 each; IX, 10; X, 6. The most dorsal tubercle on each side of abdominal somites IV-VI is reduced to a vestige; no tubercles on middorsal and midventral surfaces of abdomen and none on midventral of thorax; integument of tubercles roughened with minute (but relatively stout) spinules arranged in short transverse rows; each tubercle bearing several lateral hairs, which vary in number, size (0.002-0.036 mm) and location; a few apical or subapical sensilla and/or minute hairs. Body hairs exceedingly few, widely scattered, minute (0.015 mm long), straight and slender. Integument spinulose, the spinules minute, stout and in short rows. Cranium subhexagonal in anterior view; somewhat broader than long; dorsal to each antenna near the occipital border there is a prominent boss bearing a few sensilla and a single hair; integument of front and most of clypeus roughened with numerous minute bosses; remainder of cranium bearing minute spinules which are isolated or in short rows. Hairs of head few, minute (0.02-0.036 mm long), scattered, simple, slightly curved. Antennae a pair of low rounded eminences, each bearing three sensilla and mounted on a disc. Labrum short; breadth twice the length; strongly bilobed due to a wide median incision of the ventral border; anterior surface with a low boss (bearing several sensilla and a few minute hairs) on each ventrolateral area; ventral border of notch with transverse ridges; lateral borders of labrum with appressed scales, some of which are produced into spinules. Posterior surface of labrum: middle ⅔ spinulose, the spinules minute and arranged in numerous parallel transverse rows; lateral sixths with spinules coarse and isolated or in short arcuate rows; five or six sensilla in an irregular row extending obliquely upward from each side of the notch. Mandibles narrow and somewhat elongate; heavily sclerotized; apical tooth curved medially and posteriorly, slender in anterior view, its medial surface concave; two subapical teeth on the medial border; basal half partly spinulose, the spinules minute and isolated or in short arcuate rows. Maxillae with the apex paraboloidal and densely spinulose; spinules moderately long, coarse, stiff, sharp-pointed, in arcuate rows; palp and galea arising close together on a low lateral lobe; palp subcylindrical, slightly curved, the apex rounded and bearing four sensilla (one large and button-like); galea scarcely longer than palp, slender, subconical, bearing two apical sensilla. Labium with the anterior surface densely spinulose; apically the spinules are long, coarse, stiff, sharp and isolated; basally they are minute and arranged in short transverse rows; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are



Text fig. 2. *Neoponera obscuricornis latreillei* Forel.—Left, photomicrograph of integument of head in anterior view, ×42; right, photomicrograph of integument of mouth parts, ×70.

arranged in transverse rows; palp a frustum bearing five apical sensilla (one of which is button-like); opening of sericteries wide and salient, with three projections. Hypopharynx densely spinulose, the spinules fine and arranged in long parallel transverse rows. (Material studied: 21 larval integuments from Brazil, British Guiana and Panama Canal Zone.)

*Neoponera apicalis* (Latreille).—Plate III, fig. 13. Similar to *latreillei*, except in the following characters: Tubercles with several (typically four) longer (0.05 mm) lateral hairs; apex flat and bearing a sensillum or a minute hair; two small tubercles on abdominal somite III and two vestigial each on IV-VII. Cranium with a broad low rounded longitudinal ridge extending from the middle of the occipital border to the level of the antennae; vertex, genae and gula spinulose, the spinules minute and isolated or in short rows, but variable as to size and arrangement. Maxillary spinules on anterior surface mostly isolated, those on the posterior surface in short transverse arcuate rows. (Material studied: 12 larval integuments from Colombia and Costa Rica.)

*Neoponera villosa* (Fabricius).—Plate III, figs. 11, 12, 14 and 18. Similar to *latreillei*, except in the following characters: Tubercles shorter (0.11-0.38 mm); those on the thorax predominantly long, with the basal half cylindrical and the apical half conical; those on the abdomen predominantly short and conical; terminating in a short acute apical spine. Body hairs longer (0.027-0.072 mm). Integument of occiput spinulose, the spinules minute, those near the middle in short transverse rows, the lateral isolated. Bosses on anterior surface of labrum less prominent, with fewer sensilla. Maxillary spinules on the anterior surface in short transverse arcuate rows, those on the posterior surface isolated. (Material studied: four larval integuments from British Guiana.)

*Neoponera villosa inversa* (F. Smith).—Emery (1904) and Wheeler (1928a and 1928b, p. 205) discuss mermithergates of this ant and infer that the nematode larvae were parasitic in the ant larvae.

## Genus PACHYCONDYLA F. Smith

Body beset with numerous (118) mammiform tubercles, each with a circle of 5-10 hairs around the base; no spinules on tubercles (except on prothoracic). Young larvae have the tubercles surmounted by a stout acuminate subconical spine. Body hairs minute and restricted to ventral surface. Labrum short; ventral border concave; numerous (24) sensilla on posterior surface. Mandibles elongated and rather narrow; base stout but not dilated; surface of basal ⅔ partly spinulose, the spinules minute and in short arcuate rows. Maxillary palp and galea arising close together (but not from a lateral lobe).

Wheeler, 1910: "The larvae . . . have prominent, pointed, or rounded tubercles which probably have a protective function" (p. 74). "Larvae furnished with rows of tubercles" (p. 233). On page 234 he mentions a possible function of such tubercles—defending the larvae from one another.

Wheeler, 1928b, p. 233: "In certain Ponerinae (Pachycondyla) which are primitive, wasplike ants, the larvae when fed produce a salivary secretion which is licked up by the nurses."

*Pachycondyla striata* F. Smith.—Plate III, figs. 1-10. Shaped somewhat like a crook-neck squash. Thorax and first abdominal somite forming a long slender neck which is strongly curved ventrally; remainder of abdomen voluminous and subellipsoidal, its ventral profile nearly straight, its dorsal profile curved, its flattened ventral surface separated from its convex dorsal surface by a rounded ventrolateral longitudinal welt. A ventral welt across the anterior portion of the prothorax. Posterior end round-pointed. Anus ventral. Leg vestiges and vestigial gonopods present. Thirteen differentiated somites. Spiracles mounted on low papillae. Body beset with numerous (approximately 118) mammiform tubercles, which are arranged in 10 longitudinal rows and apportioned thus: prothorax, 10 (one pair vestigial); meso- and metathorax, 8 each; abdominal somites I-IV, 10 each; V-VII, 10 each (the dorsal pair vestigial); VIII, 10; IX, 8; X, 4; none on midventral surface. Around the base of each tubercle is a circle of 5-10 hairs which are simple, nearly straight, constricted at the base and 0.04-0.23 mm long. Body hairs few, simple, straight, minute (0.05 mm long), limited to ventral surface. Integument of tubercles smooth, except on the prothoracic where it is spinulose. Integument of prothorax and of midventral surface elsewhere spinulose, the spinules minute and isolated or in short rows. Cranium subhexagonal in anterior view, the dorsal corners rounded; as broad as long, broadest just below the antennal level; vertex and upper half of genae spinulose, the spinules minute and isolated or in short rows. Hairs of head few, short (0.035-0.088 mm), simple, nearly straight. Antennae a pair of low convexities, circular in outline and bearing three sensilla each. Labrum short, breadth 1¾X length; bilobed due to the wide shallow concavity of the ventral border; lateral border sinuate; ventrolateral borders spinulose; the anterior surface of each lobe bears about 20 sensilla and three minute hairs. Posterior surface of labrum: middle ⅔ densely spinulose, the spinules minute and arranged in numerous short subparallel transverse rows; lateral sixths sparsely spinulose, the spinules coarser and isolated or in short rows; a dozen sensilla on each lobe.

Mandible elongate and rather narrow; base stout but not dilated; apical tooth slender, acute, curved medially and posteriorly; two (rarely three) stout subapical teeth on the medial border; basal ⅔ partly spinulose, the spinules minute and arranged in short arcuate rows; sometimes a few minute blunt denticles on the medial border proximal to the subapical teeth. Maxillae with the apex paraboloidal and densely spinulose, the spinules short (longer apically), slender, sharp-pointed and isolated on the anterior surface, in short arcuate rows on the posterior surface; palp and galea arising close together on the lateral surface; palp a subcylinder bearing four or five sensilla on its flat apex; galea finger-like and bearing two apical sensilla. Labium: middle third of the anterior surface sparsely spinulose, the spinules in short rows; lateral thirds densely spinulose, the spinules isolated; spinules sharp-pointed, mostly long; on the anterior surface near the base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in transverse rows; on the posterior surface the spinules are minute and arranged in short arcuate rows; palp a moderately stout subcylinder, with four or five sensilla on its flat opex; opening of sericteries wide and salient, with three projections. Hypopharynx densely spinulose, the spinules in numerous transverse rows. (Material studied: numerous larvae from Panama Canal Zone.)

In young larvae (2.5-6 mm long) each tubercle is surmounted by a subconical spine about 0.12 mm long. This spine has a stout base but narrows rapidly to an acuminate apex; it may be straight or slightly curved. The base of the tubercle is encircled by a row of stiff slightly curved hairs about 0.14 mm long. A 6-mm larva which is ready to moult shows a mature tubercle inside each immature tubercle; the basal hairs of the former are gathered together in a bunch and inserted into the cone of the latter.

Eidmann, 1936, p. 35: "Die Larven gleichen völlig denen von *Pachycondyla harpax* Fabr., wie sie von Wheeler (1910, p. 74) abgebildet wurden. Die jungen Larven sind bedeckt von Warzen, die mit einer kräftigen, stachelartigen Spitze gekrönt sind, deren Basis von Borsten umstellt ist. Bei den älteren Larven sind die Warzän abgeflacht und ohne den stachelartigen Fortsatz, tragen aber an ihrer Peripherie in ringförmiger Anordnung Borsten. Die Mandibeln der Larven sind in allen Stadien sehr kräftig entwickelt und zweispitzig. Sie lassen auf eine Ernährung mit festen Substanzen, wahrscheinlich erbeuteten Insekten schliessen."

*Pachycondyla crassinoda* (Latreille).—The tubercles number approximately 112. The tubercle hairs are curved and are mostly longer and more numerous. The head hairs are coarser and constricted at the base. Otherwise as in *striata*. (Material studied: four larvae from British Guiana.)

Myers (1931, p. 276) records the rearing of *Kapala cuprea* Cameron from cocoons of *crassinoda*. Presumably the eucharid larva was parasitoid in the ant larva.

*Pachycondyla fuscoatra* Roger.—Emery (1904) and Wheeler (1928a & 1928b, p. 205) discuss a mermithergate of this species and infer that the nematode larva was parasitic in the ant larva.

*Pachycondyla harpax* (Fabricius).—Tubercle hairs shorter; fewer sensilla

on anterior surface of labrum; no denticles on medial border of mandibles; spinules on mandibles in longer rows; maxillae with the spinules shorter and arranged in short arcuate rows on both anterior and posterior surfaces; medial spinules of labium longer and more abundant. Otherwise as in *striata*. Material studied: two larvae from British Guiana.)

*Pachycondyla harpax montezumia* F. Smith.—Similar to *harpax*. (Material studied: seven larvae from Texas.)

Wheeler (1900a) described the larva of *montezumia* (but cited it merely as *harpax*) as "neither as slender as those of Leptogenys nor as robust as those of Odontomachus. The ventral surface of the abdomen is distinctly flattened. The head resembles that of Odontomachus, especially in the shape of the labrum and mouth-parts. There is a striking difference between the tubercles of the very young and the adult larva. In the former the tubercles are nearly or quite straight, and somewhat longer and more pointed than those of Leptogenys. They lack the terminal bristle. The bristles about the base are somewhat irregular in their insertion. In the adult larva the tubercles are reduced to large more or less flattened bosses, encircled with a regular row of numerous, rather long bristles. In the stages between those figured the gradual flattening of the juvenile spine-like tubercles can be traced through the successive moults" (pp. 17-18). Fig. 8 on p. 19: *b*, a young larva in side view; *c*, tubercle of same; *d*, mature larva in side view; *e*, head of same in anterior view. Refigured: Wheeler, 1910, Fig. 40 on p. 74.)

In the same paper Wheeler gave an account of feeding (1900a, p. 24): "Among the larvae were several pieces, one or two segments long, of a recently killed myriopod (Scutigera). Into these pieces the larvae, some of which were nearly full-grown, had inserted their heads and were devouring the softer tissues! . . . In another nest . . . I observed the larvae . . . lying on their backs, devouring the pieces of some insect which I could not identify." (Repeated by Wheeler, 1910, pp. 234-235.) (Referred to by Forel, 1923, p. 118 = 1928, vol. II, p. 300.)

Wheeler (1901a) described *montezumia* larvae as "shaped like the well-known cucurbitaceous product known as the 'crook-necked squash,' and covered with hairy tubercles" (p. 1008). But this paper deals primarily with the extraordinary phorid larvae commensal with the ant larvae: "Each of these seemed to wear about its neck a huge collar, — a sort of Elizabethan ruff, — consisting of a curled larva. That this could not be another ant-larva was apparent from a moment's examination. In all cases it almost completely encircled the ant-larva in the region of the first abdominal, or in some cases the metathoracic, segment. The posterior end was provided with a sort of disk, which adhered so tightly that both larvae could be killed in alcohol without separating" (p. 1008).

"As soon as the ants had been transferred to the Lubbock nest they were given a number of young larvae of *Camponotus sansabeanus*. These they soon proceeded to malaxate with their mandibles, twirling the morsels about in the mean time with their fore legs and lapping up the exuding juices with their tongues. Finally they deposited the crumpled and pulpy remains of the

Camponoti on the trough-like ventral surfaces of their larvae, which had been previously placed on their backs in a rough chamber dug in the earth of the nest. This chamber was immediately under the glass roof-pane, so that further developments could be closely observed with a pocket lens. Each ant-larva at once stretched forth its head eagerly and began to devour the viands with which it had just been provided. At the same moment the dipteron larva, too, as if sniffing the odor of the fresh food, unwound its tapering neck from the ventral surface of its host, and, without shifting the attachment of its posterior end, at once plunged its mandibles into the food. Under the lens both larvae could be seen greedily dining side by side till the last particle of the Camponotus larva had been consumed or prematurely removed by the worker ants.

"When the ant-larvae were huddled close together, a collar-like larva was sometimes observed to reach over and help itself from the food supply of a neighbor; but even when thus compelled to crane its neck to the utmost, it never shifted the attachment of its caudal end. Sometimes when there was no food within reach it would tweak with its sharp little jaws the sensitive hide of a neighboring ant-larva, till the latter squirmed with pain. It would sometimes even tweak its own host, as if to make it wriggle and perhaps thereby incite the worker ants to bring a fresh supply of provisions.

"The following day two living myriopods (Lithobius) were placed in the nest. During the morning hours they were killed by the Pachycondyla workers, shorn of their many legs, cut up into pieces of convenient length, malaxated, and fed to the larvae as on the preceding day. And again I was able to witness the strange banquet—the dwarf reaching down from the shoulders of the ogre and helping himself from the charger formed by the trough-like belly of his host. The same observation was repeated on several successive days. Pieces of various ant-larvae, beetle-larvae, Lithobius, Scutigera, Oniscus, —all were served up to the ant-larvae and partaken of with great relish by the dipteron larvae as well. There could be no doubt that the latter were true commensals, — perhaps the most perfect commensals, in the original meaning of the term, to be found in the whole animal kingdom!

"As one of the smallest Pachycondyla larvae, scarcely one-fourth grown, bore a very small dipteron larva, it is, perhaps, safe to say that the ant-larva acquires its commensal at a very early age. The two then grow up together, so that there is always a certain relation between the two kinds of larvae—large Pachycondyla larvae bearing large commensals, and *vice versa*. The worker ants lick and cleanse the commensals at the same time that they are caring for their own larvae. This is usually done just after meals" (pp. 1009-1010).

"First, the peculiar habits of the phorid show clearly that the ponerine method of feeding the larvae with comminuted insects is not only the typical but the only method employed by these ants, for such a commensal would certainly starve if the Pachycondyla larvae were carefully fed like the larvae of Camponotus and Formica, by regurgitation of liquid food from the mouths of the workers. The phorid profits by a peculiarity in the behavior of its

host, and thereby demonstrates—by one of Nature's experiments—that *Pachycondyla harpax* cannot feed its young by regurgitation" (p. 1015).

"The larvae bearing the commensals were certainly as large and healthy as any others in the nest, and produced perfectly normal pupae, which in the cases observed all lacked the imaginal disks for the wings and were therefore of the worker type. Whether the presence of the commensals by reducing the amount of food even to a slight degree could inhibit the development of queen larvae and thereby convert them into workers, involves a problem as interesting as it is difficult to solve in the present stage of our knowledge" (p. 1015).

Wheeler's classic illustration (1901a, Fig. 1 on p. 1009) shows the host larva lying on its back with the phorid larva wrapped around its neck. This figure has been repeated by Brues (1946, Fig. 7), Brun (1924, Fig. 51), Escherich (1902), Forel (1921b, Fig. 35 = 1928, Vol. I, Fig. 39) and Kellogg (1905, Fig. 759).

The phorid was later described by Brues (1903) as *Metopina pachycondylae*. "The larvae live as commensals with the larvae of the ant *Pachycondyla harpax Fabr.*" (p. 384).

Wheeler in 1907 (p. 44-49) repeated "in a slightly altered form" his 1901 account and published a photograph (Pl. V, fig. 69; repeated Wheeler, 1910, Fig. 243 on p. 407) of Pachycondyla and Metopina larvae.

Wheeler, 1918, pp. 295-296: "I was able to show that their peculiar tuberculate larvae are not fed with regurgitated food, like the larvae of more specialized ants, but with pieces of insects (1900). . . . An unpublished note, the significance of which I did not appreciate at the time, refers to *Pachycondyla* and was recorded while I was studying the behavior of its extraordinary Phorid commensal, *Metopina pachycondylae* (1901). It runs as follows:

" 'As soon as the fragments of insects are placed on the larva's trough-like ventral surface, the latter is sometimes inundated with a copious, colorless liquid, which is at once eagerly lapped up by the attendant nurse.'

"I should now describe this behavior in the following words: As soon as the fragments are placed on its ventral surface, the larve discharges from its salivary glands a supply of secretion which is sometimes very abundant. This secretion, by means of a strong proteolytic ferment which it contains, digests the food extraintestinally and thus enables the larva to swallow and assimilate it, and at the same time serves in part as an agreeable draught for the nurse. The strong mandibles of the Ponerine larvae are used for comminuting the insect food and thus preparing it for the action of the saliva."

Wheeler (1923a, pp. 24-25 = 1923b, pp. 221-223) has given a condensed summary of his earlier (1901) observations on Pachycondyla and Metopina and reproduced his 1907 photograph as Fig. 86 on p. 23 (= Fig. 86 on p. 222).

Wheeler (1928b, p. 254) refers to the Metopina larva as a myrmecocleptic and gives a brief abstract of his 1901 observations.

Brues (1946, p. 41) gives a brief summary of Wheeler's 1901 observations

and reproduces (Fig. 7) the classic figure. He uses the generic name Catadinusa instead of Metopina.

Brun (1924) repeats (as Fig. 51, p. 167) Wheeler's 1901 figure and states that "die Larven gewisser kleiner Fliegen (*Phoridae*) legen sich als lebende Halsbänder rings um den Nacken der Ameisenlarven an, um bei deren Fütterung mitzuprofitieren."

Forel (1921b, p. 119 = 1928, vol. I, p. 311) gives a brief summary of Wheeler's observations and reproduces the classic figure (Fig. 35 = Fig. 39).

Kellogg (1905, p. 540, based on Wheeler, 1900) discusses the feeding of *P. harpax montezumia* (see under Leptogenys below).

*Pachycondyla* sp.—Müller, 1886, pp. 90-91: "Der Kopf trägt wohlausgebildete Mandibeln, kurze stummelförmige Taster. Der Körper, an seinem vorderen Ende schlank, nach hinten stark verdickt, zeigt breite, scharf abgesetzte Bauchplatten. Die Segmente sind tief geschieden, jedes typisch gebaute trägt 10 Tuberkeln, flache Erhebungen, von denen jede mit einem Kranz von 8-10 Chitinborsten umstellt ist. Neben diesen Larven findet sich noch eine zweite Form, vielleicht die jüngeren Tiere; dieselben sind stets kleiner, unterscheiden sich bei gleicher Kopfbildung und gleichem Gesamthabitus durch die Bildung der Tuberkeln, welche verhältnismässig lange konische Erhebungen ohne Kranz von Chitinborsten sind. Sie finden sich in grösserer Anzahl (14 oder 16?) auf den typischen Segmenten. Beiderlei Larven tragen fast stets das vordere Körperende weit ventralwärts eingebogen." Fig. 2 shows a larva in side view, Fig. 3 a head in anterior view (p. 91).

The larvae described in the preceding paragraph were regarded by Müller and by Forel (1891, p. 163) as heteromorphic Eciton larvae, but they are most probably Pachycondyla larvae which had been taken in a raid. See Emery, 1900, p. 513; Wheeler and Long, 1901, pp. 168-172; G. C. Wheeler, 1943, p. 330.

### Genus BOTHROPONERA Mayr

Abdomen robust, depressed, elliptical in ventral view. Integument densely spinulose, the spinules long, with conical base and needle-like point, arranged in rows which in some places form a reticulate pattern. Tubercles few (10-38); restricted to sides of thorax and abdominal somites I or III-V; subconical; smooth or with the basal half spinulose; a few apical and/or subapical sensilla or with an apical hair. Body hairs few and minute. Head subglobular. Antennae mounted on discs. Head hairs minute. Mandibles with the base slightly enlarged; the apical half with a thickened outer edge and an inner blade off the anterior surface; basal half of posterior surface spinulose.

Wheeler (1918, p. 299 and 1922, p. 71) uses larval (as well as adult) differences to justify treating Bothroponera as a genus instead of a subgenus of Pachycondyla.

*Bothroponera sublaevis* Emery.—Pl. II, figs. 26-30. Thorax and first abdominal somite forming a moderately long and rather stout neck, which is strongly folded over toward the ventral surface; remainder of abdomen robust, depressed, elliptical in ventral view; a low rounded longitudinal welt on each side. Leg vestiges conspicuous; each a minute rounded pit at the bottom of

a larger rounded pit; wing (?) rudiments and vestigial gonopods conspicuous. Tubercles very few (10); subconical; squat to elongate; length 0.035-0.18 mm; basal half spinulose; with a few apical and/or subapical sensilla, some of which may bear a minute hair. Tubercles are found only on the lateral surfaces and are distributed thus on each half of the larva—prothorax 2, mesothorax 1, metathorax 1, first abdominal somite 1. Body practically naked; hairs very few, widely scattered, minute (length 0.03 mm). Integument densely spinulose; spinules long (0.018 mm), with stout conical base surmounted by a needle-like point; arranged in rows, which in some places form a reticulate pattern. Head moderately large, subglobular, practically naked; hairs moderately numerous but minute (length 0.006-0.018 mm). Antennae low rounded elevations, each mounted on a disc and bearing three sensilla. Labrum short; breadth twice the length; lateral borders convex, ventral sinuate; anterior surface with two ventrolateral clusters of about 20 sensilla and six minute hairs each. Posterior surface of labrum spinulose; spinules arranged in transverse subparallel rows on the medial ⅔; lateral sixths with coarser isolated spinules near the ventral border; very few sensilla. Mandibles with the basal half slightly dilated; apical half with a thickened lateral part from the anterior surface of which a blade extends medially; posterior surface of basal half with minute isolated spinules. (Material studied: two damaged integuments from Queensland.)

Wheeler, 1918: The larva of *sublaevis* has "a very broad elliptical body, with a short, stout neck, strongly folded over onto the ventral surface, which is somewhat concave. The integument is also hairless and of a peculiar opaque, gray color. The sides of the three thoracic segments and first abdominal segment are furnished with fleshy tubercles and the mouthparts are very highly developed. It is placed on its back by the nurses and fed with fragments of insects deposited on its trough-like ventral surface as in our North American Ponerinae" (p. 299). Fig. 4 on page 302: A, larva in ventral view; B, larva in side view; C, head in anterior view; D, head in side view. (Figures repeated by Wheeler 1922, Fig. 9 on p. 70; on page 56 he states that the larvae of Bothroponera are hairless.)

*Bothroponera sp.*—Pl. II, fig. 25. Tubercles few (38); subconical, squat to elongate; 0.026-0.16 mm long; the apex with a pit from the bottom of which arises a minute hair, which projects from the opening; with 0-3 subapical sensilla; spinules variable (from almost none to many on the basal half). Tubercles on the sides of the body only and distributed thus: five on each side of prothorax; one on each side of mesothorax and of the metathorax; a cluster of four on each side of abdominal somites III, IV and V. Integumentary spinules as in *sublaevis*. Body practically naked; hairs very few, widely scattered and minute (length 0.018 mm). Head as in *sublaevis* Labrum as in *sublaevis,* except lateral borders sinuate and the anterior surface of each lobe with about 12 sensilla and two minute hairs. Mandibles with the base slightly enlarged; apical half with a thickened lateral border and a median blade; the thickened outer edge terminates in a long and rather stout apical tooth, which is strongly curved medially and posteriorly, and bears one

or two subapical teeth on its anterior surface; blade terminates ventrally in a blunt apical tooth and sometimes has also a smaller subapical tooth on the inner border; posterior surface of basal half spinulose, the distal spinule exceedingly minute and arranged in transverse rows, the proximal coarser and isolated. Maxillae large; apex paraboloidal and densely spinulose, the spinules long, slender, curved, and sharp-pointed, shorter basally; palp a subcylinder with flat apex, which bears four sensilla, one of which is button-like; galea subconical, slightly curved, with two apical sensilla. Labium small; densely spinulose, the spinules long, slender, sharp-pointed and arranged in transverse rows; palp short and subcylindrical, with four apical sensilla, one of which is button-like; opening of sericteries wide and salient. Hypopharynx cordate; densely spinulose; the spinules arranged in a reticulate pattern. (Material studied: two damaged integuments from Queensland.)

*Bothroponera soror* Emery.—Eidmann (1944, p. 433) has compared this larva with *sublaevis:* "Von ihr unterscheidet sich die Larve von *B. soror* nicht unwesentlich. Vor allem ist die ventrale Einkrümmung des Vorderkörpers nicht so auffallend. Sie liegt zwar auch wie bei jener im Bereich des ersten Abdominalsegmentes, erreicht aber nur eine Abbiegung von etwa einem rechten Winkel. Ferner ist das larvale Abdomen bei weitem nicht so stark verbreitert wie bei *sublaevis,* sondern hat, wie bei den meisten Ameisenlarven, annähernd runden Querschnitt. Auch fehlen die fleischigen Fortsätze an den Seiten der 4 ersten Körpersegmente. Dafür ist die Larve jedoch stark bedornt; die einzelnen Dornen stehen auf warzenförmigen Erhöhungen." Fig. 6: E (p. 432), "erwachsene Larve"; F, head in anterior view. This larva is so different from those we have studied that we question whether it belongs in this genus at all.

Haskins (1941, p. 213) reported that the larvae of *B. soror* were fed with cut-up insect food. He found the life cycle to be: egg 15 days, larva 15 days, pupa one month.

## Genus EUPONERA Forel

It is not possible to characterize the larvae of this genus as a unit, because they fall into two very distinct types. Neither is it possible to characterize the subgenera, because larval taxonomy is not at all correlated with current adult taxonomy. Different species of the same subgenus may belong to different types, while species of different subgenera may belong to the same type.

TYPE I.—Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long slender neck, which is strongly bent ventrally; remainder of abdomen rather plump. Tubercles numerous (136); subconical, short and stout to long and slender; dorsal tubercles on abdominal somites III-VI reduced to low rounded bosses; each tubercle with minute spinules arranged in numerous transverse rows and 1-3 minute hairs near the apex. Clypeal integument not spinulose. Mandibles narrow and elongate; slightly curved; base only slightly dilated; basal half spinulose, the spinules minute and arranged in short arcuate rows.

This group includes *E.* (*Mesoponera*) *constricta* and *E.* (*Trachymesopus*)

*stigma;* also—to judge from Emery's figures—*E.* (*M.*) *caffraria.*

TYPE II.—Elongate and slender; subcircular in cross section; diameter greatest at the sixth and seventh abdominal somites, decreasing gradually toward the anterior end and only slightly toward the posterior end; thorax and one or two abdominal somites somewhat curved ventrally; remainder of abdomen straight; no clearly defined neck. Tubercles numerous (166); typically long, slender and finger-like, encircled by several rows of minute spinules; they may bear on the apex an exceedingly minute hair. A certain number of abdominal somites (two, three or five) have the dorsal pair of tubercles doorknob-shaped, i.e., a stout stalk enlarging gradually to a distal bulb; a few minute spinules on the stalk and two exceedingly minute hairs on the bulb. Clypeal integument spinulose. Mouth parts large. Mandibles elongate, narrow and slightly curved; base only slightly dilated; basal half spinulose, the spinules minute and arranged in short arcuate rows.

This group includes *E.* (*Trachymesopus*) *gilva;* also—to judge from published descriptions and figures—*E.* (*Trachymesopus*) *sauteri, E.* (*Mesoponera*) *leveillei* and *E.* (*Brachyponera*) *solitaria.* This group show more affinity to Ponera than to its alleged congeners of Type I.

Wheeler (1910, p. 233) characterizes the larvae of Trachymesopus (but under the name of Pseudoponera) as "furnished with rows of tubercles."

*Euponera* (*Mesoponera*) *constricta* (Mayr).—Plate IV, figs. 1-7. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long slender neck, which is strongly bent ventrally; remainder of abdomen rather plump, its dorsal profile moderately convex, its ventral straight; dorsal and ventral surfaces separated by a low rounded longitudinal welt; posterior end rounded. Anus ventral. Leg vestiges present. Thirteen differentiated somites. Spiracles mounted on low papillae. Body beset with numerous (136) tubercles, distributed as follows: 10 on each thoracic somite; 12 each on abdominal somites I-VIII; eight on IX; two on X. Tubercles on neck and on posterior end are long, slender and subconical; those on the rest of abdomen are shorter, stouter and more rounded apically; the most dorsal tubercles on abdominal somites III-VI are reduced to low rounded bosses; none on midventral surface. Integument of tubercles spinulose, the spinules minute and arranged in numerous transverse rows. Each tubercle bears 1-3 minute (0.006 mm long) hairs near the apex. Body hairs very few, simple, minute (0.012-0.022 mm long), on ventral surface only. Integument of ventral surface with minute spinules in transverse rows; rest of body integument very densely spinulose, the spinules minute but not in rows. Head (with mouth parts) oval in anterior view; integument of genae and dorsal part of cranium (down to level of antennae) with rather short rows of minute spinules. Head hairs few, slender, slightly curved, slightly constricted at base, short (0.045 mm). Antennae rather large, subcircular, convex; each with three sensilla. Labrum short, breadth $1\frac{3}{4}$X the length; bilobed due to a wide median incision in the ventral border; lateral borders sinuate; anterior surface of each lobe with a ventrolateral cluster of ten sensilla and two minute hairs. Posterior surface of labrum densely beset with fine spinules; those on

the middle half in numerous long subparallel transverse rows; those on the lateral quarters in short arcuate rows; four sensilla in a curved row extending obliquely upward from each side of the notch. Mandibles moderately sclerotized; elongate and narrow, with the base only slightly dilated; moderately curved medially and posteriorly; with one slender apical and two acute subapical teeth; surface of basal half spinulose, the spinules minute and arranged in transverse slightly curved rows. Maxillae conoidal; densely spinulose; spinules minute, short, slender, in short transverse rows; palp a subcylindrical peg, with four apical sensilla (one button-like); galea slender and subconical, with two apical sensilla. Labium densely spinulose; spinules in transverse rows, coarse on the anterior surface, minute on the posterior; on the anterior surface near the base there is a conspicuous transverse welt which is semicircular in profile and whose spinules are arranged in transverse rows; palp a short subcylindrical peg, its apex flat and bearing four sensilla (one button-like); opening of sericteries wide and salient, with three projections. Hypopharynx with numerous transverse subparallel rows of minute sharp spinules. (Material studied: two larvae from British Guiana.)

*Euponera* (*Mesoponera*) *caffraria* (F. Smith).—Emery, 1899, p. 5: "La parte posteriore del corpo è molto più rigonfiata e i suoi segmenti sono affatto indistinti. I tubercoli cutanei sono piccoli, acuti, subspiniformi e molto meno numerosi." Pl. I, fig. 2a, larva in side view; 2b, head enlarged, in side view.

Wheeler, 1900a, p. 15 (referring to Emery, 1899): "Mandibles powerfully developed for ant-larvae, the anterior portion of the body long and slender and folded over the abdominal portion, and . . . covered with rows of peculiar tubercles beset with more or less prominent bristles."

*Euponera* (*Mesoponera*) *leveillei* Emery.—Eidmann, 1936, pp. 35-36: "Sie sind am ganzen Körper mit Ausnahme des Kopfes ringsum mit langen fingerförmigen Höckern besetzt. Diese sind an der Spitze abgerundet und manchmal etwas verdickt und tragen auf ihrer ganzen Oberfläche mikroskopisch kleine Dörnchen, die besonders auf den distalen Teilen der Höcker eine regelmässig ringförmige Anordnung zeigen. Die Spitze trägt in der Regel einige grössere Dornen. Ausserdem befindet sich auf der Dorsalseite des 4. und 5. Abdominalsegments je ein Paar grosser, gestielter, knopfförmiger Auswüchse, ähnlich wie sie von Wheeler (1910, p. 75) bei der Larve von *Ponera coarctata* ssp. *pennsylvanica* Buckl. gefunden wurden. Ferner haben die Larven auf dem Prothorax unmittelbar hinter den Mundteilen auf jeder Seite 2 knopfförmige stumpfe Höcker und 2 Reihen ähnlicher Gebilde auf der Ventralseite des 2.-6. Abdominalsegments . . . Die knopfförmigen Papillen . . . halte ich für Exsudatorgane." Pl. I, fig. II 1 shows a larva in side view; fig. II 2 a tubercle enlarged.

*Euponera* (*Trachymesopus*) *gilva* (Roger).—Plate IV, figs. 8-16. Elongate and slender; subcircular in cross section; diameter greatest at the sixth and seventh abdominal somites, decreasing gradually toward the anterior end and only slightly toward the posterior end, which is rounded; thorax and one or two abdominal somites somewhat curved ventrally; remainder of abdomen straight; no clearly defined neck. Anus ventral. Leg vestiges present. Thir-

teen differentiated somites. Spiracles on small papillae. Body bristling with numerous (156) long (0.035-0.12 mm) slender finger-like nearly straight tubercles arranged in longitudinal rows and distributed as follows: 10 on the prothorax; 12 each on mesothorax and metathorax; 14 each on abdominal somites I and II; 12 each on III-VII; 14 each on VIII and IX; 6 on X. None on midventral surface. Each tubercle is encircled by several rows of minute spinules and may have on the apex an exceedingly minute hair (about 0.006 mm long) as well as a few spinules. In addition, the dorsum of each abdominal somite III-VII bears a pair of doorknob-shaped tubercles; each tubercle has a stout stalk which enlarges gradually to a distal bulb; shape of bulb variable in preserved specimens; the surface of the stalk bears a few minute scattered spinules; two exceedingly minute hairs on the bulb. Body hairs few, short (about 0.03 mm long), simple, restricted to the ventral surface. Integumentary spinules on the ventral surface only; minute; in short transverse rows. Cranium subhexagonal in anterior view; all corners rounded; clypeus bulging, sharply delimited by furrows; a median rounded ridge from the dorsal border of the clypeus, fading dorsally; integument of clypeal bulge spinulose, the spinules in short tranverse rows; isolated spinules on the median ridge, the vertex and the genae. Mouth parts large and conspicuous. Head hairs few but variable in number and arrangement; stout at base, apex acuminate; slightly curved near the tip or straight; short (0.035-0.07 mm long). Antennae moderately large, each with three sensilla. Labrum moderately large; breadth 1.4X length; bilobed due to a wide deep median incision of the ventral border; lateral borders sinuate; ventral border with a few spinules and four sensilla on each lobe; anterior surface with a cluster of six sensilla and two minute hairs on each lobe. Most of posterior surface densely spinulose, the spinules minute and arranged in numerous long sinuate transverse subparallel rows; ventrally and laterally the rows are broken into arcuate components; from either side of the notch a row of four sensilla extends obliquely upward and outward. Mandibles large and heavily sclerotized; narrow and elongate; base scarcely enlarged; apex slightly curved medially; apical tooth small, round-pointed; two moderately large round-pointed subapical teeth on the medial border; basal half with short transverse arcuate rows of exceedingly minute spinules. Maxillae large, conoidal, with the base constricted; apical half spinulose, the spinules minute, those near the apex in short rows, the others isolated; palp a slender cylinder with four apical sensilla, one bearing a long spine, the others a spinule; galea finger-shaped, with two apical sensilla. Labium large and prominent; spinulose, the spinules minute; those on the anterior surface in short transverse rows on the medial half, isolated on the lateral quarters; those on the posterior surface isolated distally and in short rows basally; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in short transverse rows; palp a subcylindrical peg, with four apical sensilla, two of which bear a spinule each, one a spine, while the fourth is button-like; opening of sericteries wide and salient, with three projections. Hypopharynx densely spinulose, the spinules minute and arranged in numerous long transverse

rows. (Material studied: eighteen larvae from Alabama, collected by Dr. W. S. Creighton.)

Haskins, 1931, p. 512: "Immediately upon hatching the larva is removed from the egg-mass and allowed to lie singly on the chamber floor. Not infrequently the ova and hatched larvae are kept in separate chambers, and a rough division of the larval brood according to size is usual, but not rigidly maintained. The larvae are fed with bits of solid food in the usual Ponerine fashion, and are active and athletic, and wholly entomophagous. They are surprisingly sensitive. Not infrequently, when food was introduced at the entrance to an artificial nest, larvae uncurled and stretched their long necks in search of it. It is possible that this action resulted from an association of light, perceived through the general integument, with the fact of food as previously experienced. The adults of the colony spend much time in licking the larvae for exudates and also apparently for saliva. This food, indeed, seems normally to constitute the entire diet of the callows for the first few days. The adults frequently pinch the larvae vigorously about the neck and abdomen, apparently to hasten and encourage the flow of exudates. When mature, the larvae are carefully covered entirely with earth in the usual manner, and spin at once. The earth is removed as soon as the first sheet of silk is completed, and the cocoon is cleaned within a short time." The life cycle is given (pp. 512-513) as egg 30-31 days, larva 22-35 days and pupa 31-33 days.

*Euponera* (*Trachymesopus*) *sauteri* (Wheeler).—Teranishi, 1927 (translated from the Japanese by two university students): "This larva, closely related to Ponera, has glutinous tubercles on the dorsal surface of abdominal somites III to VII inclusive, one pair on each somite. In addition there is a pair of bristle-capped tubercles on the dorsal surface of each somite and two pairs on each lateral surface. All other somites, except the most anterior, have two pairs on the dorsal surface and two pairs on each lateral surface. The first somite has only one pair of bristle-capped tubercles on the dorsal surface; like the others it has two pairs on each lateral surface. The number and function of the glutinous dorsal tubercles do not change as the larva matures. The neck region of the larva is long and hook-shaped.

"The above species was formerly known as a Pseudoponera in the genus Pachycondyla until C. Emery (Genera Insec., Ponerinae, p. 84, 1911) classified it under Trachymesopus in the genus Euponera. After studying the position of the glutinous dorsal tubercles in the young larva of *sauteri*, I fully agree with Emery in separating it from Pachycondyla, but I am not convinced that it should be placed in Euponera" (p. 298).

"The neck and mouth parts are well developed because these larvae reach for their own food, which is placed near them by the workers" (p. 300). "The function of the glutinous dorsal tubercles is to attach the larva to the walls or ceiling of the nest" (p. 297). "At present it is believed that the bristle-capped tubercles prevent the larvae from eating each other" (p. 300). Fig. 4 on p. 299—a nearly full-grown larva in side view.

*Euponera* (*Trachymesopus*) *stigma* (Fabricius).—Similar to *Mesoponera constricta* but differing in the following respects: The tubercles number the

same (136) but are distributed differently: 12 on each thoracic somite; 14 each on abdominal somites I and II; 12 each on III and IV; 10 each on V-VIII; 6 on IX; 2 on X. Integumentary spinules on ventral surface only. Head hairs exceedingly minute (about 0.009 mm long). Lateral borders of labrum convex. Mandibles with dorsal subapical tooth stouter. Maxillary palp with two apical and one button-like subapical sensilla. Labial palp with four apical and one subapical sensilla. Hypopharynx cordate. (Material studied: numerous larvae from British Guiana and Costa Rica.)

The young larva (length 2 mm) of this species is only slightly curved ventrally and has the posterior part only slightly enlarged. There is no differentiated neck. The posterior end is round-pointed and directed ventrally. The number and distribution of the tubercles is the same as in the mature larva; those on the prothorax and mesothorax and on the venter of the abdomen are conoidal; those on the metathorax and on the lateral longitudinal welts are paraboloidal; those on dorsum of the abdomen are subhemispherical. There is a rounded transverse welt on the dorsal surface of each abdominal somite IV-VII.

*Euponera* (*Trachymesopus*) *stigma* var. *quadridentata* (F. Smith).—Emery, 1899, pp. 4-5: "Il corpo ha una porzione anteriore più sottile, coi segmenti ben distinti e una posteriore rigonfiata, in cui non si vedono limiti distinti tra i segmenti, il loro numero essendo indicato dalle stigme e, negli stadi più inoltrati, dalle sporgenze segmentali o tubercoli del tegumento. Come in generale, nelle larve degli Imenotteri, le stigme sono al numero di 10 paia e mancano nel 1° segmento che segue il capo, nonchè nei due ultimi segmenti della regione addominale. Nello stadio più giovane, si vedono solo deboli accenni dei tubercoli cutanei; ritengo che questo stadio debba corrispondere alle larve di prima schiusa e che lo stadio seguente, di poco più grande, sia quello che segue la prima muta. In esso appariscono, già ben distinti, parte dei tubercoli; questi si fanno successivamente più numerosi e sporgenti, a misura che la larva cresce. La mie figure faranno riconoscere la loro distribuzione e la grandezza relativa. Osservati a forte ingrandimento, i tubercoli più acuti della regione toracico hanno forma conica, troncata all'apice e portano ciascuno alcuni brevi peli. Del resto, il corpo di queste larve è quasi totalmente destituto di peli.

"Il capo è relativamente molto sviluppato e subgloboso; sotto il labbro superiore appariscono le mandibole, molto più grandi che non siano nelle larve di *Formica* e *Camponotus;* esse sono in buona parte scoperte nella loro faccia laterale, e sporgono in avanti, terminate con tre piccoli denti. . . . Le mascelle hanno alla loro faccia laterale due prolungamenti chitinosi conici, giallognoli, dei quali quello più vicino all'apice è più grande e diretto innanze. Il labbro inferiore ha due paia di simili coni più piccoli e più pallidi, e nel mezzo una papilla o filiera che riceve lo sbocco delle ghiandole della seta. Le parti boccali hanno del resto struttura quasi identica a quella che si osserva nella larva di *Odontomachus*." (Wheeler, 1900a, p. 18, footnote: the third and fourth sentence quoted.) "La forma di queste larve e i tubercoli spiniformi che si trovano sulle più grandi di esse parvero anche a me singolari" (p. 4). Pl.

I, fig. 1a, b, c—three different stages in development of the larva, drawn to the same scale; d—a dorsal tubercle from the first somite, enlarged. (Fig. 1c copied by Berlese, 1925, Fig. 825B on p. 846.)

In this same article Emery quoted (p. 4) a note from Professor L. Biró concerning the same larvae: "'Nelle gallerie del nido scavate nel legno putrido, si trovavano le larve dal lungo collo, coperte di spine singolari: abbandonate dai loro vigliacchi custodi, quelle larve sapevano difendersi da sè; quando qualche termite (il nido di queste trovavasi nello stesso legno) si avvicìnava ad una di esse, questa batteva innanzi e indietro col suo collo di cigno e tosto veniva lasciata in pace.'" Wheeler (1910, p. 234), referring to the above, says that Biró "saw these larvae, when disturbed by some termites, move their long necks back and forth with sufficient force to drive away the intruders." Emery (1911, p. 53): "M. le Prof. Biró a observé à la Nouvelle-Guinée que les larves de *Euponera stigma,* Fabricius, en agitant leur col de cygne, étaient capable d'effrayer des termites qui voulaient en faire leur proie."

Wheeler (1900a, p. 15) refers to Emery's description, making the same comments as under *Eu.* (*M.*) *caffraria* above.

*Euponera* (*Brachyponera*) *lutea* (Mayr).—Wheeler, 1933, p. 99: "I have not seen the larvae of *lutea* devouring insect food and am therefore inclined to believe that they may be fed with liquids by regurgitation." This hypothesis has been confirmed by Haskins and Haskins (1950, p. 7).

*Euponera* (*Brachyponera*) *solitaria* (F. Smith).—Teranishi,, 1927 (translated from the Japanese by two university students): "There is one pair of glutinous tubercles on each of abdominal somites II-IV. The other somites have, instead of glutinous dorsal tubercles, a pair of bristle-capped tubercles on the dorsal surface and five on each lateral surface, whereas somites II-IV have five bristle-capped tubercles on each lateral surface only. When the larva is in the third instar (I am not certain about the exact age) the glutinous dorsal tubercles on the second abdominal somite disappear; those on the third and fourth move posteriorly and assume a different position. . . . Those of the third somite are larger than those of the fourth. Those of both somites are, however, shorter than those of the previous stage. The anterior portion of the body bends downward. . . . The abdominal somites are not very distinct" (p. 298). "The neck and mouth parts are well developed because these larvae reach for their own food, which is placed near them by the workers" (p. 300). "The function of the glutinous dorsal tubercles is to attach the larvae to the walls or ceiling of the nest" (p. 297). "At present it is believed that the bristle-capped tubercles prevent the larvae from eating each other" (p. 300). Fig. 2—second (?) instar larva in side view; Fig. 3—dorsum of abdominal somites II-V in side view (p. 299).

## Genus CRYPTOPONE

Tubercles numerous; typically slender, elongate and subcylindrical; basal third slightly constricted, its integument smooth; distal 2/3 encircled by a few

rows of spinules; apex surmounted by a hemispherical cap which is encircled by a row of spinules. Doorknob-shaped tubercles also present. Body hairs moderately abundant. Body hairs and head hairs with the distal third denticulate. Cranium short; transversely subelliptical in anterior view. Antennae small. Labrum short; anterior surface with two minute hairs but no sensilla; ventral border with four sensilla on each lobe. Mandibles with a few arcuate rows of fine spinules on the basal half. Galea spinulose.

*Cryptopone mayri* Mann.—Plate III, figs. 20-26. Body beset with numerous tubercles, most of which are slender, elongate, subcylindrical (but with the basal third slightly constricted), encircled by a few rows of minute spinules (none on basal third) and having the apex surmounted by a hemispherical cap which is encircled by a row of spinules. There are also doorknob-shaped tubercles, somewhat similar to those of Ponera. Body hairs slender, straight and short (length about 0.045 mm), the distal third roughened with minute denticles. Cranium transversely subelliptical in anterior view. Head hairs moderately numerous, short (0.03-0.06 mm); distal third with minute denticles. Labrum short, breadth twice the length; bilobed due to a wide shallow median incision of the ventral border; lateral borders sinuate; ventral border with four sensilla on each lobe; the anterior surface of each lobe bears two minute hairs but no sensilla. Posterior surface of labrum with numerous subparallel transverse rows of minute spinules, except near the lateral borders where there are only a few scattered arcuate rows; two sensilla near the center of each lobe. Mandibles moderately sclerotized; slightly enlarged at base; curved medially; apex slightly curved posteriorly; apical tooth rather small, round-pointed, curved medially; two small, round-pointed subapical teeth arising from a narrow mesal blade; basal half with short transverse rows of minute spinules. Maxillae large, lobose, round-pointed; apex bearing minute spinules arranged in short rows; palp a subcylindrical peg, with a few isolated spinules on its surface and with three apical sensilla (two of which bear each a spinule); galea slender, elongate, subconical, with a few short transverse rows of minute spinules on its surface and with two apical sensilla. Labium narrow; anterior surface with numerous minute spinules arranged in short transverse rows; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in transverse rows; palp a subcylindrical peg with three apical and one subapical sensilla; opening of sericteries wide and salient with two projections. (Material studied: one head integument and fragments of body integument from the Solomon Islands.)

### Genus PONERA Latreille

Without a sharply differentiated neck; thorax stout; abdomen scarcely enlarged. Integument of ventral surface finely spinulose; lateral and dorsal surfaces coarsely and conspicuously spinulose. Tubercles numerous (164-184) typically spire-like; each encircled by a few rows of minute spinules and surmounted by a long and rather stout spine-like hair. There are also on the dorsal surface of certain abdominal somites two to four pairs of doorknob-

shaped tubercles, one pair on a somite. Cranium suboctagonal in anterior view; its integument spinulose on the genae, vertex and middle of front. Antennae subhemispherical. Labrum with one to three sensilla on the ventral border of each lobe. Mandibles rather long and narrow; base only slightly dilated; apical half consisting of a thicker outer part and a narrow mesal blade; basal half sparsely spinulose, the spinules minute and in short transverse arcuate rows.

Donisthorpe (1915, p. 68 = 1927a, p. 69): "*Head* fairly large, with strong horny mandibles, body clothed with bristle capped tubercles, and four pairs of glutinous club-shaped tubercles, situated on the dorsal part of the sixth and following somites."

Wheeler, 1910: The larva of Ponera has "prominent, pointed . . . tubercles which probably have a protective function, and in addition to these . . . pairs of glutinous dorsal tubercles which . . . serve to attach the larva to the walls of the nest" (p. 74). "Larvae furnished with rows of tubercles" (p. 233). "Some of the species of *Ponera* also have long cylindrical dorsal tubercles which are glutinous at their ends and serve to anchor the larva to the walls of the nest" (p. 234). It is possible that the bristly tubercles "are used in defending the larvae from one another, for the larvae, like the adults, are highly carnivorous and when food is scarce probably attack one another" (p. 234).

*Ponera coarctata pennsylvanica* Buckley.—Plate V, figs. 18-21 and 28-32. Without a well differentiated neck; diameter greatest at the fifth and sixth abdominal somites, decreasing gradually toward the anterior end and more abruptly toward the posterior end; thorax and first two abdominal somites stout and curved ventrally, remainder of abdomen nearly straight; ventral surface slightly flattened and separated from the more rounded dorsal surface by a feebly developed longitudinal welt; posterior end rounded. Anus ventral. Thirteen differentiated somites. Body beset with numerous (156) tubercles distributed as follows: prothorax, 10; mesothorax, 12; metathorax, 12; abdominal somites, I, II, VII and VIII, 14 each; III-VI, 12 each; IX, 12; X, 6; none on the midventral surface. These tubercles are spire-like; each is encircled by a few rows of minute spinules and is surmounted by a rather long and stout spine which arises by an articulation from an apical depression; length (including spine) 0.04-0.11 mm. In addition, there is also a pair of doorknob-like glutinous tubercles on the dorsum of each abdominal somite III-VI; each consists of a stout column bearing an inflated knob; shape of knob variable; length about 0.11 mm. Body hairs few, simple, straight, minute to short (length 0.018-0.072 mm); limited to ventral surface. Head moderately large; cranium suboctagonal in anterior view; integument spinulose on the middle of the front (down to the level of the antennae), on the vertex and on the genae; spinules minute, mostly isolated but some in rows; mouth parts moderately large. Head hairs moderately numerous, short (0.035-0.07 mm), simple, slightly curved. Antennae moderately large; subhemispherical; each with three sensilla. Labrum: breadth 1¾ X length; strongly bilobed due to a wide deep incision of the ventral border; lateral borders sinuate;

near its ventral border each lobe bears on its anterior surface two minute hairs and about five sensilla; 1-3 sensilla on the ventral border of each lobe. Posterior surface of labrum densely spinulose; spinules minute; on the median half arranged in numerous subparallel transverse rows; on the lateral quarters sparser and in short arcuate rows; two or three sensilla near the middle of each lobe. Mandibles moderately sclerotized; rather long and narrow; base only slightly dilated; apical half consisting of a thicker outer part and a narrow inner blade; apical tooth prominent, strongly curved medially, slightly curved posteriorly; two stout subapical teeth arising from the blade; basal half sparsely spinulose, the spinules minute, in short transverse arcuate rows; on the posterior surface near the subapical teeth there are a few coarse spinules. Maxillae large; bulging at the sides; apex paraboloidal and densely spinulose; the spinules minute and in short arcuate rows; rest of surface sparsely and irregularly spinulose; palp a frustum, with four apical sensilla (three bearing each a spinule and one a small cone) and one button-like subapical sensillum; galea finger-like, with two apical sensilla, each bearing a spinule. Labium prominent; spinulose, the spinules arranged in short transverse rows, except at the sides, where they are isolated; palp a short frustum bearing four apical (each surmounted by a spinule) and one button-like subapical sensilla; opening of sericteries wide and salient, with three projections. Hypopharynx densely spinulose, the spinules minute, in long curved transverse rows. (Material studied: numerous larvae from Illinois, Michigan and New Hampshire.)

Young larvae resemble mature larvae, except that the head and tubercles are relatively larger and the body curvature is less.

Our observations on living larvae show that the glutinous tubercles are really sticky. When a single tubercle was touched with a dissecting needle it adhered to the latter so firmly that the larva (length about 1.8 mm) was picked up by merely lifting the needle; it remained thus suspended. A larva was caused to adhere to the ceiling of a glass cell by means of its four posterior tubercles.

Wheeler, 1900b, pp. 52-53: "The larva is clearly of the Ponerine type. . . . It is rather robust, with a large head succeeded by five distinct segments. The remaining segments, forming the swollen abdomen, are not distinctly marked off from one another. The body is furnished with outgrowths of three different types. The first of these is represented by a number of pointed bristles confined to the ventral surface of each segment. The second type is represented by several longitudinal rows of pointed tubercles, each of which, under a high magnification is seen to consist of a short distal spine and a long, tapering proximal base, directly continuous with the integument of the larva, and covered with transverse rows of serrated points. The distal spine is movably articulated with the proximal portion, and is so easily detached that it may be overlooked. The third type of projection is found only on the dorsal surface of the third to sixth abdominal segments as four pairs of club-shaped structures which are glutinous to the touch. That these are peculiar modifications of the tapering tubercles seems to be indicated by the fact that they

replace on either side in each of the four above-mentioned segments the more posterior of the two pointed projections seen in the thoracic, first and second, and seventh and eighth abdominal segments. The larva is usually kept on its back, so that the four pairs of glutinous tubercles act as suckers and fix it to the sides of the earthen chamber or to the glass of the artificial nest. The ants have to exert a slight effort in pulling the larva away from its attachment. The head . . . is broad, evenly rounded behind, and beset with short stiff bristles. The labrum is bilobed and does not extend beyond the tips of the powerful tridentate mandibles. The fleshy maxillae and labrum [labium] project somewhat beyond the mandibles, the former being provided with robust tactile cones, the latter with a prominent median tubercle on which opens the duct of the spinning gland. Comparison of the figures in this and my previous paper shows that the larva of *P. coarctata* is peculiar in lacking the circlets of bristles on the pointed projections and in possessing clavate adhesive tubercles on the dorsal surface of the abdomen.

"The larvae are fed in the very same manner as the larvae of the large Texan Ponerinae, *i.e.*, with pieces of food and not with liquid regurgitated by the ants. In confinement I did not succeed in inducing the ants to feed their larvae with fragments of insects, but they carried crumbs of moistened corn bread to them, and the larvae could be seen lying on their backs, attached by their glutinous dorsal tubercles, slowly consuming the morsels which had been placed on their flattened ventral surfaces. The fixation of the larva to the walls of the nest seems to be an adaptation for giving freer play to the head and slender neck during feeding." Fig. 4 on p. 52: *a,* larva nearly ready to pupate; *b,* bristle-capped tubercle of same; *c,* head in anterior view. Figure repeated by Wheeler, 1910, Fig. 41 on p. 75; by Escherich, 1906, Fig. 30 = 1917, Fig. 360).

Eidmann (1936, p. 36 and 1944, p. 438) refers briefly to the larva of *pennsylvanica;* he regards the fungiform tubercles as exudate organs.

Escherich (1917, p. 96-97) refers briefly to the four pairs of "keulenförmiger klebriger Fortsätze auf dem Rücken;" he regards them as organs of attachment ("Haftorgane").

*Ponera coarctata* (Latreille).—Donisthorpe (1927b, p. 72) records the staphylinid beetle, *Lamprinus saginatus* Gr. as a "hostile persecuted lodger" with the ant. "Both the adult beetle and their larvae devour the ants' eggs, larvae, and pupae."

*Ponera foeda* Forel.—Wheeler, 1901b, p. 200: "Larvae similar to those of *P. opaciceps.*"

*Ponera japonica* Wheeler.—Teranishi, 1927 (translated from the Japanese by two university students): "On the ventral side of the larva there are segments. On the dorsal surface of the fourth, fifth and sixth abdominal somites there are glutinous tubercles, one pair on each. Surrounding these dorsal tubercles and generally scattered over the body are numerous bristle-capped tubercles. At the anterior end the first and second somites bend directly downward. Behind this bend the thorax forms an arc. The above remarks refer to the young larva" (p. 298). "The neck and mouth parts are well

developed because these larvae reach for their own food which is placed near them by the workers" (p. 300). "The function of the glutinous dorsal tubercles is to attach the larva to the walls or ceiling of the nest" (p. 297). "At present it is believed that the bristle-capped tubercles prevent the larvae from eating each other" (p. 300). Fig. 1—first (?) instar larva (p. 299).

*Ponera opaciceps* Mayr.—Wheeler, 1901b, p. 199: The larvae resemble those of *coarctata* [*pennsylvanica*] except that they "have fewer pairs of dorsal adhesive tubercles."

*Ponera* sp.—Pl. V, fig. 33. Apparently similar in general to *pennsylvanica* but differing in the following characters: The spire-like tubercles are stouter; only two pairs of doorknob-like glutinuos tubercles, which are located on abdominal somites IV and V. No integumentary spinules on the ventral surface. On either side of the ventral surface of the prothorax there is a large flap-like outgrowth; each bears a small hair and a sensillum but no integumentary spinules. These flaps are unique among the ant larvae we have studied. It is therefore unfortunate that a more precise identification cannot be made; we have no adult ants; our material includes only the damaged integuments of three larvae accompanied by the label "Ponera sp. N.S.W."

*Ponera* sp.—Pl. V, figs. 22-27. Generally similar to *pennsylvanica* but differing in the following respects: Spire-like tubercles more numerous. There are only 2 pairs of glutinous doorknob-shaped tubercles, one pair each on abdominal somites IV and V; they are much stouter; the integument of the stalk has several transverse rows of minute spinules. In addition there is a pair of ventrolateral projections on the prothorax; these are paraboloidal; each bears two hairs (about 0.045 mm long); they are not found on *pennsylvanica* but are in the same position as the flaps of the New South Wales species described above. The body integument has finer spinules on the ventral surface, while those on the dorsum are longer and more acuminate. Head hairs fewer and shorter. Integument of head not spinulose. Labrum twice as broad as long; lateral borders spinulose; each half of posterior surface with three or four sensilla near the base. Apical and subapical teeth of mandibles smaller; apical tooth less curved; no spinules near subapical teeth. Maxillae conoidal. Spinules on labium short but in longer rows.

A single living larva of this species was observed in an artificial formicary. The whole body glistened as if its integument was wet. The larva usually lay on its side, but when stiumlated it rolled onto its belly, stretched its neck forward, applied its mouth parts to the filter paper (on which it was lying) and pulled itself forward by a shortening and hunching of the neck. The glutinous tubercles (on their stalks) were waved about in all directions. The knobs were filled with a clear fluid and their shape was changeable, apparently by means of pressure changes in this fluid. Once while creeping the knobs of the two posterior glutinous tubercles chanced to touch an overhanging bit of damp soil. The knobs adhered to the soil; the anterior end of the body was held suspended and consequently the larva was unable to progress; it wriggled vigorously but could not free itself.

The above observations and description are based on two larvae and two

semipupae found with workers in soil in flower pots in the Biology Department greenhouse at the University of North Dakota, Grand Forks, North Dakota, May 3, 1950 (No. 417) and May 24, 1950 (No. 418). Dr. M. R. Smith of the United States National Museum has kindly examined some of the workers and written us as follows: "The ants collected from your Department greenhouse on May 3 and 22 appear to be the same species of *Ponera*. They are, however, neither *coarctata* Latr. nor *coarctata pennsylvanica* Buckley. Those two forms are easily distinguished from your greenhouse specimens in that their heads are much more coarsely punctate and their petiolar nodes of an entirely different shape when viewed posterodorsally. I have compared your specimens with other determined forms in our collection, but have not found anything with which they are identical. Could your greenhouse form have been introduced? The ants are certainly different from all other recorded North American forms with which I am familiar. Thanks for the gift of the specimens. If I am ever able to name them I will write you."

### Genus TRAPEZIOPELTA Mayr

Tubercles moderately numerous (about 90); subconical, with the apex rounded; each tubercle may bear one or two minute hairs and those on the abdomen have a few minute spinules on the apex; otherwise the integument is smooth. Head hairs exceedingly minute, mostly below the level of the antennae. Labrum subquadrate or subtrapezoidal (i.e., not bilobed); posterior surface with the spinules on the middle half (or third or $^3/_5$) rather long and arranged in short to moderately long transverse combs; posterior surface with 16 sensilla grouped in four clusters. Mandibles directed ventrally, completely exposed (or nearly so); long and slender; base only slightly enlarged; apical third strongly curved posteriorly and terminating in a long slender curved acute apical tooth; a few minute spinules on the inner surface, some longer, sharp-pointed and isolated, other exceedingly minute and in short transverse rows. Maxillary palp chair-shaped, the "seat" with two sensilla (one cup-shaped and one bearing a small cone), the apex with two apical sensilla (each bearing a spinule). Labial palp elongate (longer than maxillary palp), subconical, with the apical third skewed to one side, bearing two lateral (one button-like and one bearing a small cone) and two apical sensilla.

*Trapeziopelta* sp.—Plate IV, figs. 17-31. Shaped somewhat like a crookneck squash; thorax and first abdominal somite forming a long slender subcylindrical neck which is strongly bent ventrally; rest of abdomen swollen and subovoidal, its dorsal profile strongly convex, its nearly straight ventral and lateral profiles meeting at right angles; diameter greatest at the sixth abdominal somite. Leg vestiges present. Anus ventral. Thirteen differentiated somites. Body beset with 92 tubercles which are arranged in longitudinal rows on the dorsal and lateral surfaces (none ventral) and distributed as follows: six each on abdominal somites V, VI and IX; two on X; eight each on all other somites. Tubercles subconical, with the apex rounded; those on the thorax relatively slender and 0.075-0.17 mm long, those of the abdomen stouter and ranging in height from 0.075 to 0.19 mm; each tubercle may bear one or two minute (0.018 mm) hairs; the abdominal tubercles have a few

minute integumentary spinules on the apex. Body hairs few, simple, slightly curved, minute (length 0.018-0.07 mm); widely scattered, except on the rather densely hirsute dorsa of abdominal somites IV-VII. Dorsa of posterior abdominal somites and ventral surface of thorax spinulose; spinules exceedingly minute and arranged in short rows; on either side of each abdominal somite there is a dorsolateral and a ventrolateral integumentary structure of unknown nature and function. Head moderately large; cranium subhexagonal in anterior view, but with the occipital border strongly rounded; mouth parts moderately large. Head hairs few, simple, straight, exceedingly minute (length about 0.009 mm); mostly below the level of the antennae. Antennae rather large elliptical, scarcely elevated; each with three sensilla. Labrum subquadrate; ventral corners rounded; on either side the anterior surface shows a low convexity bearing two minute hairs and about eight sensilla. Posterior surface of labrum densely spinulose; on the median half of the spinules are slender, acuminate and rather long and arranged in short to moderately long transverse combs; on the lateral quarters the spinules are smaller and arranged in short rows or isolated; two groups of sensilla at each side of the medial half—three in a cluster at the middle and five in a basal cluster. Mandibles directed ventrally; completely exposed (or nearly so); moderately sclerotized; long and slender; base only slightly enlarged; apical third strongly curved posteriorly and terminating in a long slender curved acute apical tooth; two short blunt subapical teeth on the inner border; a few minute spinules on the inner surface, some longer, sharp-pointed and isolated, others exceedingly minute and in short transverse rows. Maxillae large; apex conoidal and sparsely spinulose, the spinules coarse, sharp-pointed and isolated; palp chair-shaped, the "seat" with two sensilla (one cup-shaped and one bearing a small cone), the apex with two apical sensilla (each bearing a spinule); galea an elongate truncate cone with two sensilla on its flat apex. Labium wide and prominent; anterior surface spinulose, the spinules longer and in short rows mediobasally, shorter and isolated laterally and distally; on the anterior surface near the base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in short transverse rows; palp elongate (longer than maxillary palp), subconical, with the apical third skewed on one side, bearing two lateral (one button-like and one bearing a small cone) and two apical sensilla; opening of sericteries wide and salient with three projections. Hypopharynx densely and coarsely spinulose, the spinules arranged in transverse rows. (Material studied: two larvae—7 mm long—labelled "British N. Borneo E. Mjöberg.")

*Trapezoipelta* sp.—Labrum subtrapezoidal, slightly narrowed ventrally; slightly broader than long; anterior surface has six sensilla on each convexity; eight sensilla on the ventral border; posterior surface with combs on the middle third. Otherwise similar to the larvae described above. (Material studied: two semipupae—7 mm long—labelled "Mt. Dulit 3000 ft. Br. N. Borneo E. Mjöberg.")

*Trapezoipelta* sp.—Generally similar to the larvae described first above but differing in the following characters: Tubercles fewer (88) and distrib-

uted as follows: eight each on prothorax and abdominal somites I-III; ten each on mesothorax and metathorax; six each in IV-VIII; four on IX; two on X. All tubercles similar, hemispherical, each bearing an exceedingly minute (about 0.006 mm long) hair. Body hairs exceedingly minute (length 0.009-0.018 mm); no dense patch on the dorsum. Integumentary spinules limited to ventral surface of thorax. Labrum with four sensilla on the ventral border; posterior surface with combs on the middle $^3/_5$; spinules on the outer fifths more numerous and in longer rows. Maxillary spinules shorter and in short transverse rows. (Material studied: one semipupa—6 mm long—labelled "Mt. Penrissen, Sarawak Altitude 2000 f. leg. Dr. E. Mjöberg.")

### Tribe ONYCHOMYRMICINI Ashmead

### Genus ONYCHOMYRMEX Emery

Moderately stout; constricted at the first abdominal somite; diameter increasing both anteriorly and posteriorly from this constriction; diameter greatest at the sixth abdominal somite. Thorax slightly bent ventrally; abdomen straight. Anus subterminal. No tubercles. Body hairs moderately abundant and uniformly distributed; head hairs very few. Antennae large, with 2-4 sensilla each. Labrum small; not bilobed; subtrapezoidal, narrowed below; several sensilla on or near the ventral and lateral borders; no hairs on the anterior surface; posterior surface sparsely spinulose, the spinules minute and in subparallel rows extending outward and upward from the middle; posterior surface with several sensilla near the ventral border and a median cluster near the base. Mandibles long and narrow; basal $^2/_5$ somewhat enlarged; distal $^3/_5$ very slender, with the apex strongly curved posteriorly (but not medially) and terminating in a slender curved acute apical tooth; two small blunt denticles on the mesal border; no spinules. Maxillae sparsely spinulose; palp a low elliptical elevation furnished with four sensilla (one a frustum, one bearing a finger-like process, and two with a spinule each). Labium with the anterior surface sparsely spinulose; palp a low elevation bearing four sensilla.

Wheeler, 1916, p. 47: "Slender, smooth and nontuberculate, with twelve very distinct postcephalic segments, the constrictions between which are everywhere deep and conspicuous, even at the posterior end of the body. Head short, rounded, with well-developed, slender, acute, falcate mandibles, destitute of teeth. Clypeus rather long, projecting. Antennae very small. Maxillary sensillae long and prominent. Head sparsely, remainder of body more densely and uniformly covered with short, straight, stiff hairs or bristles."

Whenever we examine a larva of Onychomyrmex, we are inclined to exclaim, "How did that get in here?" It certainly does not belong among the higher ponerine larvae. In fact, it hardly belongs among the Ponerinae at all. Apparently a somewhat similar attitude has been held toward the adults. True, the genus has usually been in the tribe Ponerini, but actually it has been *incertae sedis*. Emery in the "Genera Insectorum" says, "La place de ce genre singulier dans la section des Euponerinae et la tribu des Ponerini est provisoire. Tant que le mâle sera inconnu, l'on ne pourra prononcer un jugement fondé sur ses affinités véritables" (1911, p. 97). Wheeler (1916)

expresses a similar opinion but adds, "The larva of Onychomyrmex, in the very distinct segmentation of the body and in the structure of the head, seems to be of a rather primitive type and resembles the larvae of the Dorylinae (Eciton) and lower Ponerinae [now Cerapachyinae] (Acanthostichus, Cerapachys), but the larvae of ants have not been sufficiently studied to enable us to draw satisfactory conclusions concerning the phylogenetic relationships of the various genera" (p. 49).

Although we do not wish to draw any conclusions on phylogeny, we can nevertheless confirm the first part of Wheeler's statement. The larva of Onychomyrmex resembles doryline larvae in the following respects: body nearly straight, but with the anterior end slightly curved ventrally; segmentation distinct; spiracles small; body hairs short, simple and moderately abundant; labrum small; palps poorly developed, not peg-like; trophorhinium poorly developed. It differs from the Dorylinae in not being slender, subcylindrical and progressively attenuated toward the anterior end; in its better developed mandibles; and in having very few head hairs.

The larva of Onychomyrmex resembles the larvae of the Cerapachyinae in the following characters: body constricted at the first abdominal somite, the diameter increasing in both directions from this constriction (as in Eusphinctus and Lioponera, but not in Cerapachys); segmentation distinct; spiracles small; head hairs few, short and simple; labrum small; mandibles not heavily sclerotized; base of mandibles moderately enlarged, the rest long and slender; palps poorly developed, not peg-like; trophorhinium poorly developed. It differs from the cerapachyines in not being slender, nor subcylindrical nor evenly curved ventrally; in having simple body hairs; in not having the mesal borders of the mandibles serrate.

Ashmead (Can. Ent. 37: 382. 1905) regarded the genus Onychomyrmex as constituting a distinct tribe of Ponerinae (Onychomyrmicini). Wheeler (Bull. Am. Mus. Nat. Hist. 45: 638. 1922) gave it the same status in his "Keys to the Genera and Subgenera of Ants." In this we heartily concur; if it must be in the Ponerinae, it certainly should not be in the tribe Ponerini. It differs from the larvae of other genera of this tribe in not having a clearly differentiated neck which is strongly curved or bent ventrally; in lacking tubercles on the body; in having the body hairs moderately abundant (instead of few), in having 2-4 sensilla on each antenna instead of the typical three; in having a small labrum, which is not bilobed; in the shape of the mandibles and their lack of spinules; in the poorly developed palps, which are not peg-like; in the non-salient opening of the sericteries; in the poorly developed trophorhinium.

On the whole we find that the larva of Onychomyrmex shows a closer affinity to the Cerapachyinae than to any other group we have studied.

*Onychomyrmex mjöbergi* Forel.—Plate VI, figs. 1-7. Moderately stout; constricted at the first abdominal somite; diameter increasing both anteriorly and posteriorly from this constriction; diameter greatest at the sixth abdominal somite. Thorax slightly bent ventrally; abdomen straight; a low longitudinal welt on each side of the abdomen. Posterior end rounded. Anus subterminal. Leg vestiges present. Spiracles small. Segmentation conspicu-

ous, with deep furrows between the thirteen differentiated somites. No tubercles. Body hairs moderately numerous and uniformly distributed; simple, straight or slightly curved, rather stout, acute; short (about 0.035 mm). Integument of the anterior portion of the ventral surface of each thoracic somite with minute spinules in short transverse rows. Head moderately large and suboval; no integumentary spinules. Head hairs very few, widely scattered, simple, nearly straight, stout, acute; short (0.009-0.045 mm). Antennae large, elliptical, only slightly elevated; each with 2-4 sensilla. Labrum small, subtrapezoidal, narrowed ventrally; width about $1\frac{1}{4}$X length; about 14 sensilla on the ventral and lateral borders or near them on the anterior surface; posterior surface sparsely spinulose, the spinules minute and arranged in subparallel rows (of various lengths) extending obliquely outward and upward from the middle; posterior surface with a few scattered sensilla near the ventral border and a median cluster near the base. Mandibles long and narrow; moderately sclerotized; basal $^2/_5$ somewhat enlarged; distal $^3/_5$ very slender, with the apex strongly curved posteriorly (but not medially) and terminating in a slender curved acute apical tooth; two small blunt denticles on the mesal border; no spinules. Maxillae bulging laterally; apex conoidal and sparsely spinulose; spinules minute and arranged in short transverse rows; palp a low elliptical elevation furnished with four sensilla (one a frustum, two bearing each a small spine and one bearing a finger-like process); galea finger-like, with two apical sensilla. Labium with the anterior surface sparsely spinulose, the spinules coarse and isolated; palp a low elevation beset with four sensilla (one button-like and three bearing a spinule each); opening of sericteries wide but not salient, with three projections. (Material studied: numerous larvae from Queensland.)

Wheeler, 1916: Pl. 1, fig. 7—mature larva in side view; Pl. 2, fig. 1—head in side view, enlarged; Pl. 2, fig. 1a—mandible, enlarged; Pl. 2, fig. 2—head in anterior view.

### Tribe LEPTOGENYINI Forel

### Genus LEPTOGENYS Roger

Neck long and slender, strongly curved or bent ventrally; abdomen elongate, moderately slender, straight, subcircular in cross section. Tubercles numerous (134); mammiform; encircled by a subapical ring of 4-6 relatively long hairs; integument smooth. Tubercles of young larvae pointed. Integument of body densely spinulose. Head rather small; cranium subhexagonal in anterior view; slightly longer than broad; genae bulging at the middle; no integumentary spinules. Antennae large. Head hairs exceedingly minute. Labrum small and narrow, not bilobed; numerous (16-30) sensilla and/or minute hairs on anterior surface, posterior surface sparsely spinulose, the spinules in three patches; ventral border with conspicuous sensilla. Mandibles stout, elongate-subconical, with the apex rounded; a small subapical denticle which projects posteriorly; no apical or medial teeth; middle of mesal and posterior surfaces roughened with denticles. Maxillary palp chair-shaped, with two sensilla on the "seat" (one button-like and one bearing a small cone) and two on the apex (each bearing a spinule).

Wheeler (1903, p. 207) refers to the manner of carrying the larvae "by the neck, with the long slender body extending back between the legs of the worker" (as in *Cerapachys augustae* and Eciton).

Wheeler (1910): "The body [of Lobopelta] is more cylindrical" (p. 72). The larvae of Lobopelta "have prominent, pointed, or rounded tubercles which probably have a protective function" (p. 74). "Larvae furnished with rows of tubercles" (p. 233). On page 234 he mentions a possible function of such tubercles—defending the larvae from one another.

*Leptogenys* (*Leptogenys*) sp.—Plate VI, figs. 12-21. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long slender neck which is strongly curved or bent ventrally; rest of abdomen elongate, moderately slender, straight, subcircular in cross section, the ventral surface only slightly flattened, the ventral profile straight, the dorsal slightly curved; posterior end rounded. Anus ventral. Leg vestiges present. Body beset with numerous (134) mammiform tubercles arranged in longitudinal rows and distributed as follows; prothorax, 8; mesothorax and metathorax, each with 10 (two of which are vestigial); abdominal somites I-VIII, 12 each; IX, 8; X, 2; none on ventral surface of thorax or midventral surface of abdomen; height of tubercles 0.07-0.09 mm (higher on abdomen); each tubercle encircles by a subapical ring of 4-6 relatively long (0.15 mm) simple curved hairs, which are constricted at the base; integument smooth. Body hairs very few, widely scattered, simple, straight or slightly curved, minute (about 0.009-0.04 mm long), restricted to the ventral surface. Integument of body densely spinulose; spinules on ventral surface of thorax and midventral surface of abdomen minute and in long transverse subparallel rows; elsewhere they are coarse and not in rows. Head rather small; narrow and elongate; cranium subhexagonal in anterior view, slightly longer than wide; genae bulging at the middle. Head practically naked; head hairs few, simple, minute (about 0.005 mm long), widely and irregularly scattered; no spinules. Antennae high on head; large subelliptical convexities; each with three sensilla. Labrum small; slightly broader than long; widest at the middle, narrowed above and below; anterior surface with about 20 sensilla; ventral border with six frustum-shaped projections each bearing an apical sensillum. Posterior surface of labrum with three spinulose areas—one mediobasal (but with a narrow extension down the middle) and two ventrolateral; spinules mostly minute and arranged in short arcuate rows; two clusters of sensilla (four in each) near the center. Mandibles moderately sclerotized; stout; elongate-subconical; apex rounded; on the posterior surface a small subapical denticle which projects posteriorly; no apical or medial teeth; middle third of mesal and posterior surfaces roughened with denticles. Maxillae conoidal; apical portion spinulose, the spinules isolated and thick-based; palp chair-shaped, with two sensilla on the "seat" (one button-like and one bearing a small cone) and two on the apex (each bearing a spinule); galea finger-like, with two apical sensilla. Labium large; anterior surface spinulose; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in short transverse rows; palp a subcylindrical peg

with the apical third skewed on one side, with two apical (each bearing a spinule) and two subapical (one button-like and one bearing a smaill cone) sensilla; opening of sericteries wide and salient, with three projections. (Material studied: five larvae from Barro Colorado Island, Panama Canal Zone, collected July 20, 1924, by G. C. Wheeler, No. 119; the drawing of the mature larva in side view is based on a specimen collected at Columbiana Farm, Santa Clara, Costa Rica, June 21, 1924, by G. C. Wheeler, No. 43.)

The young larvae of the above species have the body more slender and the posterior end more pointed. Apparently each tubercle is produced apically into a long slender sharp-pointed spine-like process which is very fragile and usually broken or lacking in preserved specimens.

*Leptogenys* (*Lobopelta*) *elongata* (Buckley).—Plate VI, figs. 8-10. In general like the above species of the subgenus Leptogenys, but differing in the following characters: Body hairs shorter, slenderer and more numerous. All integumentary spinules smaller, the more minute on the ventral and lateral surfaces, the larger on the dorsal. Labrum subtrapezoidal; width at base slightly greater than the length; strongly narrowed but greatly thickened ventrally; anterior surface with about 16 sensilla and/or minute hairs, which are scattered irregularly; from the ventral border project a pair of palp-like structure, each bearing two apical and two posterior sensilla. The mandibles have a longitudinal posterior blade from which the subapical denticle projects. Maxillary and labial palp with the apex more slender. (Material studied: a single damaged integument from Texas, supplemented by Wheeler's figures.)

Wheeler (1900a, p. 16) describes the larvae of the above species as "remarkably slender and scarcely flattened on the ventral surface. In the young larvae the tubercles are distinctly curved and pointed, without apical bristle, and with only a few rather short bristles encircling the base. In the adult larvae the tubercles are larger and shorter, with blunt or acuminate apex and with relatively longer and more numerous basal bristles. The head of the adult larva is remarkable for its length and the narrowness of the labrum, which is nearly as long as the slender mandibles and provided with a median tooth at its tip." Fig. 7 on p. 18: *a*, young larva and *b*, mature larva, in side view; *c*, head of mature larva in anterior view; *d*, tubercle of young and *e*, of mature larva. (This figure is repeated by Wheeler, 1910, as Fig. 39 on p. 73.) "These ants decapitated termite nymphs or cut off their abdomens and scattered these about among their larvae. . . . The larvae had inserted their long necks through the cut surfaces into the soft parts of the termites and were feeding exactly like the larvae of Pachycondyla" (p. 24; repeated 1910, p. 235).

Forel (1921a, Fig. 1A on p. 23 = 1928, Vol. I, Fig. 1A on p. 23): mature larva in side view (after Wheeler). On p. 23 (1921) he describes the larva as "allongée, très mobile, avec la peau couverte de tubercules, avec une tête bien marquée et fournie de mandibules ou pinces." (= 1928, Vol. I, p. 23; "long and very mobile and which has a skin covered with tubercles and a well-defined head furnished with mandibles or nippers.")

Forel (1923, p. 118 = 1928,Vol. II, p. 300) refers briefly to Wheeler's observations on feeding (see under Odontomachus below). On page 116

(= 1928, vol. II, p. 298) he cites Fig. 1A (1921a) to exemplify the larvae of the subfamily (see under Ponerinae below).

Kellogg (1905, p. 540) refers to Wheeler's observations on *L. elongata, Pachycondyla harpax montezumia* and *Odontomachus haematoda clarus*: "The larvae were fed simply by giving them pieces of freshly killed insects which they chewed and devoured by means of their unusually well-developed mandibles. This method of larval feeding is more primitive (demands less care and manipulation on the part of the workers) than in the case of any other ants, — indeed of any other social insects, for even the wasps, which also feed their young pieces of insects, masticate these insect morsels thoroughly before turning them over to the tender larvae."

Wheeler (1918, p. 295): "I was able to show that their peculiar tuberculate larvae are not fed with regurgitated food, like the larvae of the more specialized ants, but with pieces of insects (1900)."

*Leptogenys* (*Lobopelta*) *neutralis* Forel.—Wheeler (1933, p. 87) refers to the "slender, long-necked, tuberculate larvae" (p. 87) and states (p. 88) that they are fed on entire or dismembered insects. Deälated females of *Crematogaster* (*Orthocrema*) *dispar* Forel. "had been cut in two at the petiole and only the succulent gasters given to the larvae, which inserted their slender necks into the opening at the anterior end."

*Leptogenys* (*Odontopelta*) *turneri* Forel.—Pl. VI, fig. 11. In general like the species of *Leptogenys s. str.* described above but differing in the following characters: Tubercles more elongate. The integumentary spinules, which are restricted to the ventral surface of the thorax, are minute and arranged in short transverse subparallel rows. Labrum long and narrow, the breadth at the base being only about seven-tenths the length; subtrapezoidal; lateral borders sinuate, with the distal third spinulose; ventral border rounded and bearing two clusters of three sensilla each; anterior surface with about 30 sensilla and/or minute hairs. Maxillae with the spinules between the palp and galea minute and in long transverse rows; palp with its apex more rounded and bearing five or six sensilla. (Material studied: seven larvae from Queensland.)

### Tribe ODONTOMACHINI Mayr

### Genus ANOCHETUS Mayr

### Subgenus ANOCHETUS Mayr

Neck long and somewhat stout; abdomen straight and rather stout. Tubercles moderately numerous (92). The majority of the tubercles consist of a subconical base bearing 4-6 (usually 5) relatively long hairs; on this base is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair; integument of distal cone with short transverse rows of spinules. On the middorsal surface of the abdomen there are two circular structures, one on somite IV and one on V; they may be considerably elevated and pulley-like or thin discs or merely differentiated areas that are scarcely perceptible in profile; the integument of their dorsal surfaces is glabrous. No integumentary spinules on cranium. Each antennae a low convex area surmounted by a smaller rounded projection bearing three sensilla. Labrum a little broader

than long; bilobed due to a wide and moderately deep incision of the ventral border. Mandibles rather long and narrow, with the base slightly enlarged and the apex slightly curved medially; teeth small and round-pointed; basal half of anterior surface spinulose, the spinules minute and arranged in short transverse arcuate rows. Integument of galea beset with a few minute spinules.

Wheeler, 1910—"Larvae furnished with rows of tubercles" (p. 233). On page 234 he mentions a possible function of such tubercles—defending the larvae from one another.

*Anochetus* (*Anochetus*) sp.—Pl. V, figs. 1-11. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long stout neck, which is bent ventrally; the rest of the abdomen straight and rather stout, its diameter greatest at the sixth abdominal somite, its ventral surface nearly flat and with a straight profile, its dorsal surface strongly rounded and with a curved profile; posterior end rounded. Anus ventral, with a conspicuous posterior lip. Leg vestiges present. Prothorax with a rounded swelling on each side, which bears a few minute hairs on its anterior face. Thirteen differentiated somites. Body beset with 92 tubercles distributed thus: Prothorax—10; mesothorax, metathorax and abdominal somites II, III, VI, VII and VIII—8 each; I, IV, V and IX—6 each; X—2; none on midventral surface nor on the dorsa of IV and V. A typical tubercle consists of a subconical base bearing 4-6 (usually 5) relatively long (0.18-0.25 mm) slender simple hairs, which are constricted at the point of attachment; on the apex of this basal cone is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair about 0.12 mm long; over-all length about 0.3-0.38 mm; integument of distal cone with short transverse rows of spinules. The ventrolateral tubercles on the thorax (one pair on each somite) are atypical: they are much smaller; they are not differentiated into two cones; and each bears only one or two hairs. On the middorsal surface of the abdomen there are two large discoidal elevations (one on somite IV and one on V); each might be compared to a pulley with one of its sides fused with the body wall; six or seven simple long (about 0.14 mm) slender hairs arise from the groove on each side (none from the front or back); integument of its dorsal surface glabrous. Body hairs very few; limited to ventral surface; widely scattered, except for a cluster on the prothorax; simple, straight and very short (0.018-0.07 mm); immediately in front of the anus there are a few longer hairs (0.108). Integument of ventral surface sparsely spinulose, the spinules exceedingly minute and mostly arranged in short transverse rows; rest of integument with fine grooves (?) which form a reticulate pattern; scattered irregularly along these grooves are a few exceedingly minute spinules. Head subpyriform in anterior view; cranium slightly broader than long; mouth parts prominent; gula moderately spinulose, the spinules minute and in short transverse rows. Head hairs few, simple, slightly curved, short (0.036-0.06 mm), widely scattered. Each antenna a low convex area surmounted by a smaller rounded projection bearing three apical sensilla. Labrum a little broader than long; narrowed at the base; bilobed, due to a wide and moderately deep incision of the ventral border; each lobe bearing on its ante-

rior surface a short hair and about six sensilla; lateral margins sinuate; posterior surface with numerous fine spinules arranged in short transverse rows (except on the lateral quarters where they are in short arcuate rows) and with two sensilla near the center of each lobe. Mandibles heavily sclerotized; subtriangular in anterior view; rather long and narrow; base slightly enlarged; apex slightly curved medially; apical and two subapical (on mesal surface) teeth small and round-pointed; basal half of anterior surface spinulose, the spinules minute and arranged in short transverse arcuate rows. Maxillae with the apex conoidal and spinulose; palp an elongate cylinder bearing four apical sensilla (one button-like, three bearing a spinule each); galea fingerlike, with two apical sensilla, its integument beset with a few minute spinules. Labium spinulose, the spinules coarse to fine and mostly isolated; on the anterior surface near the base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in short transverse rows; palp a slender truncate cone bearing four apical sensilla (one button-like, three bearing a spinule each); opening of sericteries wide and salient, with three projections. Hypopharynx spinulose, the spinules arranged in short transverse rows. (Material studied: seven immature larvae (4.8 mm long) labelled "Tobang Borneo 1300 m E. Mjöberg.")

We have two larvae (unaccompanied by their ants) labelled "Anochetus British Guiana." One is immature (4.8 mm long) and one mature (6.4 mm long). A comparison with our Borneo material shows that they are in the subgenus Anochetus, but there are differences. The immature larva differs from the Borneo specimens (described above) in having raised discs instead of "pulleys" on the dorsa of abdominal somites IV and V; the discs are about half as high, but their diameter is greater, in fact nearly equal to the length of the somite. In the mature larva these discs are depressed to mere circular areas which are scarcely perceptible in profile.

### Subgenus STENOMYRMEX Mayr

Tubercles moderately numerous (94). The majority of the tubercles consist of a subconical base bearing 4-9 (usually 6) relatively long hairs; on this base is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair. On the middorsal surface of abdominal somite IV there is a pair of glabrous subcircular scarcely elevated areas; another pair of such areas on V. Gula densely spinulose. Each antenna a low convex area surmounted by a smaller rounded projection bearing three sensilla. Labrum short; breadth twice the length; subtrapezoidal, narrowed at the base; ventral border nearly straight. Mandibles falciform, with one or two denticles on the mesal face at the base of the long slender sharp-pointed apical tooth; middle third of anterior and posterior surfaces spinulose, the spinules minute and grouped in short transverse arcuate rows. Galea spinulose.

*Anochetus* (*Stenomyrmex*) *emarginatus* (Fabricius).—Plate V, figs. 12, 13 and 15-17. Prothorax with a rounded swelling on each side which bears a few hairs on its anterior face. Leg and gonopod vestiges present. Thirteen differentiated somites. Spiracles on minute papillae. Body beset with 94

tubercles, which are distributed thus: prothorax—10; mesothorax, metathorax and abdominal somites I-III and VI-VIII—8 each; IV, V and IX—6 each; X—2; none on ventral surface nor on dorsa of IV and V. Each tubercle consists of a subconical base bearing 4-9 (usually 6) relatively long (0.19-0.22 mm) slender simple hairs, which are constricted at the point of attachment; on this base is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair about 0.15 mm long; over-all length 0.25-0.4 mm. The ventrolateral tubercles on the thorax (one pair on each somite) are atypical: they are much smaller; they are not differentiated into two cones; and they bear only one or two hairs. On the middorsal surface of abdominal somite IV there is a pair of glabrous subcircular scarcely elevated areas; each area is fringed anteriorly, laterally and posteriorly (but not medially) by 5-8 short (about 0.07 mm) slender simple hairs; another pair of such areas on V. Body hairs few; mostly limited to ventral surface; widely scattered, except for a cluster on the prothorax; simple, slightly curved; length moderate (0.1 mm). Integument of dorsal surface with numerous long fine transverse grooves (?) and sparsely beset with spinules; ventral surface thickly beset with minute blunt spinules which are isolated or in short transverse rows. Cranium transversely subelliptical; gula densely spinulose, the spinules minute and arranged in short transverse rows. Head hairs few, simple, slightly curved, scattered, moderately long (0.07-0.1 mm). Each antenna a low convex area surmounted by a smaller rounded projection bearing three apical sensilla. Labrum short and broad; breadth more than twice the length; subtrapezoidal, narrowed at the base; ventral border nearly straight, spinulose and bearing several sensilla; anterior surface with minute spinules in transverse rows near the middle and near the ventral border, two hairs at each side of the spinulose area and a cluster of six sensilla near each ventral corner. Posterior surface of labrum with numerous fine spinules in short transverse rows, except near the lateral borders where the rows are irregularly arranged; two sensilla on each half. Mandibles falciform, with one or two denticles on the mesal face at the base of the long slender sharp-pointed apical tooth; moderately sclerotized; middle third of anterior and posterior surfaces spinulose, the spinules minute and grouped in short transverse arcuate rows. Maxillae with the apex conoidal and spinulose; palp an elongate cylinder with a fungiform sensillum arising from an apical pit, the rim of which bears three papillae; galea finger-like, its surface bearing spinules and its apex two sensilla (each with a spinule). Labium spinulose, the spinules coarse to fine and mostly isolated; on the anterior surface near the base there is a conspicuous transverse welt which is semicircular in profile and whose spinules are arranged in short transverse rows; palp a slender truncate cone with four apical sensilla (one button-like and three bearing a spinule each); opening of sericteries wide and salient, with three projections. Hypopharynx spinulose, the spinules in short transverse rows. (Material studied: four semipupae from British Guiana.)

*Anochetus* (*Stenomyrmex*) *emarginatus rugosus* Emery.—Plate V, fig. 14. Apparently similar to *emarginatus s. str.* but differing as follows: Body hairs longer (0.1-0.2 mm). On the dorsal surface of abdominal somites IV and V

the integument shows fine grooves (?) in a reticulate pattern; scattered irregularly along these grooves are a few exceedingly minute spinules. Head hairs longer (0.09-0.13 mm). Apical tooth of mandibles more acute. The maxillary palp (as well as the galea) has its surface spinulose. (Material studied: three damaged integuments from Brazil.)

*Anochetus* (*Stenomyrmex*) *emarginatus testaceus* Forel.—Apparently similar to *emarginatus s. str.* but differing as follows: Tubercles fewer (80); none atypical. Integumentary spinules mostly confined to the thorax. Head hairs shorter (0.05-0.07 mm). (Material studied: three damaged integuments from Puerto Rico.)

## Genus ODONTOMACHUS Latreille

Neck long and rather stout; abdomen straight and somewhat swollen. Tubercles numerous (94-112). The majority of the tubercles consist of a subconical base bearing 3-14 relatively long hairs; on this base is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair; integument of distal cone with short transverse rows of spinules. On the middorsal surface of abdominal somite IV there is a pair of glabrous scarcely elevated areas; another pair of such areas on V. Gula spinulose. Antennae small. Labrum bilobed due to a moderately deep incision of the ventral border; breadth 1½X length. Mandibles moderately long and narrow; scarcely enlarged at base; only slightly curved; one apical and two subapical teeth on the mesal surface; all teeth rather large and prominent, heavily sclerotized, subequal, acute and round-pointed; surface of basal half roughened with short transverse arcuate spinulose ridges.

Clausen, 1940, p. 221: Kapala "appears to be most frequently associated with" Odontomachus. Eucharid larvae are parasitoid in ant larvae.

Wheeler, 1904, p. 767: "The larva of *Odontomachus* is much like that of the typical genus *Ponera*."

Wheeler, 1910: "Larvae furnished with rows of tubercles" (p. 233). On page 234 he mentions a possible function of such tubercles—defending the larvae from one another.

*Odontomachus haematoda* (Linnaeus).—Pl. VI, figs. 22-29. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long and rather stout neck which is strongly bent or curved ventrally; rest of abdomen somewhat swollen, nearly straight, the ventral profile nearly straight, the dorsal slightly curved; posterior end rounded. Anus ventral. Leg, wing and gonopod vestiges present. Thirteen differentiated somites. Spiracles on minute papillae. Body beset with numerous (112) tubercles, distributed thus: 10 each on prothorax and abdominal somites I-III and VI-VIII; 8 each on mesothorax, metathorax, IV, V and IX; 2 on X. Of the tubercles just enumerated the following pairs are atypical: ventrolateral on each thoracic somite; dorsolateral on I-IX; dorsal on VI. No tubercles on midventral surface nor on the dorsa of IV and V. A typical tubercle consists of a subconical base bearing 3-6 relatively long (0.16-0.2 mm) slender nearly straight simple hairs, which are constricted at the point of attachment; on this

base is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair about 0.16 mm long; over-all height 0.38 mm; the distal cone bears a few minute spinules on its surface. The atypical thoracic tubercles are small paraboloids, bearing each two short (0.036 mm) hairs; the atypical tubercles on the abdomen are small cones, bearing each an apical hair 0.36 mm long; the pair on IX is represented only by two hairs each. On the middorsal surface of IV there is a pair of contiguous glabrous scarcely elevated areas which is irregularly fringed by about a dozen slender simple short (0.03 mm) hairs; a similar pair on V. Around each of these structures are a few minute spinules arranged in concentric rows; ventral and middorsal (except IV and V) surfaces of each abdominal somite with a patch of exceedingly minute spinules in short transverse rows. Body hairs very few; on ventral surface only; widely scattered, except for a cluster on the prothorax; simple, slightly curved, constricted at the base; very short (0.036-0.09 mm). Head moderately large; cranium transversely subelliptical in anterior view; mouth parts prominent; integument of gula with short transverse rows of minute spinules. Head hairs few, scattered, simple, slightly curved, constricted at the base, short (0.045-0.09 mm). Antennae small; each with three sensilla. Labrum bilobed due to a moderately deep median incision of the ventral border; breadth 1½X the length; constricted at the base; lateral borders sinuate; ventrolateral borders spinulose; ventral border with about six large and four small sensilla; anterior surface of each lobe with two small hairs and about seven sensilla. Posterior surface of labrum with numerous rather long transverse rows of fine spinules on the middle ⅔; lateral sixths with the rows short and scattered; spinules near the ventrolateral corners more numerous and isolated or in short arcuate rows; a cluster of sensilla near the center of each lobe. Mandibles moderately sclerotized; moderately long and narrow; only slightly curved medially and posteriorly; one apical and two subapical teeth on the mesal surface; all teeth rather large and prominent, heavily sclerotized, subequal, acute and round-pointed; surface of basal half roughened with short transverse arcuate spinulose ridges. Maxillae prominent; apex paraboloidal and densely spinulose, the spinules minute, some isolated, others in short transverse rows; palp a subcylindrical peg with four sensilla (one button-like and three bearing spinules) on its flat apex; galea finger-like, with a few scattered spinules near the base and two sensilla on the apex. Labium prominent; densely spinulose, the spinules minute; on the anterior surface the medial spinules are in short rows, the rest isolated; on the posterior surface they are in short transverse rows; palp a slender subcylindrical peg bearing four apical sensilla (one button-like and three bearing spinules); opening of sericteries wide and salient, with three projections. Hypopharynx cordate, with numerous fine spinules in long transverse rows. (Material studied: fourteen larvae from Costa Rica and Jamaica.)

Clausen (1941, p. 57) lists *Chalcura deprivata* (Walker) and *Schizaspidia convergens* (Walker) as parasitoid on this species in Ceylon. Presumably the eucharid larvae were parasitic on the ant larvae.

Eidmann, 1944: "Die Larven sind durch den dünnen, langen, fast

rechtwinklig abgebogenen Thorakalabschnitt ausgezeichnet, der wie ein langer Flaschenhals an dem ampullenartig verdickten Abdomen sitzt. Ihr Körper ist mit grossen Höckern bedeckt, die aus einem dicken Basalabschnitt bestehen, der ringsum mit langen Borsten besetzt ist und eine dünne spitze Papille mit langer Endborste trägt. Bei den Eilarven fehlt der beborstete Basalabschnitt dieser Höcker. Dagegen tragen sie auf der Dorsalseite des 4. und 5. Abdominalsegmentes je ein Paar knopfförmiger Papillen" (p. 438). Fig. 9 on p. 437 shows an egg, a very young larva ("Eilarve"), the tubercle of a mature larva (enlarged), a mature larva and a cocoon.

Emery, 1899: "Le larve di *Odontomachus haematoda* rassomigliano alle precedenti per la forma e per la mancanza di limiti esterni fra i segmenti addominali. I tubercoli sono disposti con ordine più regolare, in serie trasverse, sopra i singoli segmenti. Ciascuno di essi consta di un corpo rotondeggiante, nel mezzo del quale si eleva un prolungamento conico, terminato da un pelo; sulla parte basale ritondata, sono impiantati 4-5 peli, di rado un numero minore, che fanno corona al cono piligero centrale" (p. 5). Pl. I, fig. 4: *a*, mature larva in side view; *b*, thoracic tubercle (enlarged); *c*, mandibles and labrum in anterior view; *d*, maxilla and labium in anterior view.

Emery (1904) and Wheeler (1928a and 1928b, p. 205) discuss mermithergates of *haematoda* and infer that the nematode larvae were parasitic in the ant larvae.

Haskins and Haskins, 1950, p. 4: A young fertilized queen of this species, isolated in an artificial nest, "produced numerous eggs, hatched them, and evidently fed the resulting larvae with ingluvial food (although the process was difficult to observe) since they developed rapidly."

Wheeler, 1900a, p. 15 (referring to Emery, 1899): "Mandibles powerfully developed for ant-larvae, the anterior portion of the body long and slender and folded over the abdominal portion, and . . . with rows of peculiar tubercles set with more or less prominent bristles."

*Odontomachus haematoda clarus* Roger.—Wheeler, 1900a: "The young larva of *O. haematodes* is represented in Fig. 5, *a*, which shows the arrangement and character of the bristly tubercles and the neck-like anterior portion, consisting of the head, the three thoracic and the first two abdominal segments. The remaining eight abdominal segments are much enlarged and flattened ventrally. The larva is kept on its back, and the neck-like anterior portion rests against the flattened ventral surface. The shape of the tubercles, each of which is tipped with a rigid bristle and encircled with bristles, is shown in Fig. 5, *b*. The larva was about to moult, so that the tubercle of the succeeding cuticle is seen shining through the old one. The adult larva is shown in Fig. 6, *a*. Compared with that of the young larva, its head is very small in proportion to the body. This seems to be the universal rule in ant larvae. The head in dorsal view is represented enlarged in Fig. 6, *b*. The powerful dentate mandibles lie just below the outer edges of the bilobed labrum; still lower and projecting forward lies the labium, bearing on its tip the opening of the spinning gland (to be used in weaving the cocoon), and on either side two

peg-shaped tactile (?) organs. Similar but somewhat larger organs are seen on the edges of the maxillae, which protrude on either side below the mandibles. The ten tracheal stigmata, beginning on the mesothoracic and terminating on the eighth abdominal segment, are clearly shown in Fig. 6, *a*. The bristly tubercles are essentially the same in structure as those of the younger larva, but they are relatively shorter and smaller" (pp. 15-16). Fig. 5 on p. 16: *a*, young larva in side view; *b*, tubercle. Fig. 6 on p. 17: *a*, mature larva in side view; *b*, head in anterior view; *c*, tubercle.

"During the month of May I had frequent opportunity to see Odontomachus feeding its larvae in my artificial nests. These larvae are placed by the ants on their broad backs, and their heads and necks are folded over onto the concave ventral surface, which serves as a table or trough on which the food is placed by the workers. The following observations are transcribed from my notebook:

"May 13. This evening several house-flies, placed in the Janet nest of *O. haematodes*, were at once shorn of their legs, then decapitated, and finally their thoraces and abdomens were cut into smaller pieces and distributed among the larvae. One was given a fly's head, which it kept twirling around in a comical manner, while it devoured the brain through the small cervical orifice. Another was given a piece of a thorax with one of the wings still attached, another a piece of an abdomen, still another, a leg with a mass of muscle at its coxal end, etc.

"May 16. This evening a small homopterous insect was placed in the Odontomachus nest. One of the ants (A) snapped at it, disabled it, and then left it. A few moments later it was picked up by another ant (B) and carried into the chamber containing the larvae and pupae. Thereupon a third ant (C) took hold of it and began tugging at it with B till it was torn open, but not into pieces. B then placed it on the flat ventral surface of a medium-sized larva, which began feeding at once, moving the homopteron around with its jaws. After four minutes had elapsed, another ant (D) that had been standing near by, apparently much interested in the feeding, suddenly tore the morsel away and placed it on a small larva. This larva was permitted to feed ten minutes, closely watched during all this time by ant D and another (E) which had come up in the mean time. Then ant D tried to tear the morsel away from the small larva, but apparently unable to do so, it took up the larva with the morsel and dumped them both on the ventral surface of a large larva. This creature seized the homopteron and forced the small larva to release its hold and to drop to the ground. The large larva fed for fully twenty minutes, closely watched by ant D and two others (E and F). All of these ants tried at different times to wrench the morsel away from the larva, but failed. Suddenly a small ant (G) rushed up, tore it away, and ran off with it. By this time very little was left of the homopteron and I lost track of it.

"May 23. A few crumbs of cake, moistened with water, were placed in the Odontomachus nest at 11.7 P.M. A worker soon carried one of the crumbs into the breeding chamber and gave it to a large larva at 11.20. This larva fed but a few moments, but the cake was not removed till 11.35, when

it was carried into another chamber, then at once brought back and placed between three larvae, from one of which it had just been taken. The smallest of these three larvae nibbled at it for a short time, beginning at 11.40. But one minute later this larva was carried away by a worker, and the cake was taken by another worker and given to a small larva at 11.43. This larva, too, was soon carried away (at 11.48)), and the cake was taken to a large larva, which would have none of it. It was not removed, however, till 11.50. Then it was given by another worker to a large larva, which did eat some of it. At 11.51 the piece of cake, but little diminished in size after all its perambulations, was taken to another large larva. The ant remained over the larva holding the cake in place till 11.58 when another worker came up and ran away with the larva. While the larvae were feeding, the ants themselves could be plainly seen to partake of the cake from time to time. During the whole period of the above observations, and for some minutes later, *i.e.*, for over an hour, one little larva was permitted to feed without interruption on what seemed to be a piece of a house-fly" (pp. 24-26). (Repeated Wheeler, 1910, pp. 235-237.)

Wheeler, 1918, p. 295: "I was able to show that their peculiar tuberculate larvae are not fed with regurgitated food, like the larvae of more specialized ants, but with pieces of insects (1900). Concerning the feeding of the Odontomachus larva I published the following remark (p. 24):

" 'These larvae are placed by the ants on their broad backs, and their heads and necks are folded over onto the concave ventral surface, which serves as a table or trough on which the food is placed by the workers.' "

Escherich (1906, Fig. 30 = 1917, Fig. 36B) refigures Wheeler, 1900a, Fig. 5a.

Forel, 1923, p. 118: Wheeler "a entre autres observé en appareil comment les *Pachycondyla,* les *Lobopelta* et les *Odontomachus* ☿ apportent des insectes, mis en pièces par elles, à leurs larves qu'elles surveillent pendant que celles-ci dévorent ces proies. Quand une larve a à peu près terminé son repas, la pièce d'insecte est portée à une autre et ainsi de suite." (= Forel, 1928, Vol. II, p. 300: Wheeler "has observed among other things the way in which *Pachycondyla, Lobopelta* and *Odontomachus* in an apparatus bring their larvae insects which they themselves have cut into pieces, and watch the young creatures devour their prey. When one larva has nearly finished its meal, the piece of insect is carried to another, and so forth.")

Kellogg (1905, p. 540) refers to Wheeler's observations (1900a) on feeding the larvae (see under Leptogenys above).

*Odontomachus haematoda erythrocephala* Emery.—Very similar to *haematoda s. str.* The hairs on the tubercles are somewhat longer in *erythrocephala* and the spinules or the anterior surface of the labium are mostly in rows. (Material studied: seven larvae from Panama.)

*Odontomachus haematoda insularis* var. *pallens* Wheeler. — Clausen (1941, p. 57) lists *Kapala terminalis* Ashmead and *Kapala* sp. as parasitoid on this ant in Cuba. Clausen, 1940, p. 227: "The planidia of *K. terminalis* are usually found attached to the throat of the *Odontomachus* larvae, somewhat to one side. Transfer to the pupa is effected just prior to the first molt

of the parasite, and the appendages of the pupa never attain more than half their full length."

*Odontomachus haematoda pubescens* var. *bruneipes* Emery.—Eidmann, 1936, p. 37: "Die Larven sind ausgezeichnet durch den dünnen und langen, fast rechtwinklig abgebogenen Thoracalabschnitt, der wie ein langer Hals an dem ampullenartig verdickten Abdomen zu sitzen scheint. Der Körper ist bedeckt mit grossen Höckern, die aus einem dicken Basalabschnitt bestehen, der ringsum mit langen Borsten besetzt ist, und der wiederum eine dünne spitze Papille mit langer Endborste trägt. Die durchaus ähnlich gestaltete Larve der Stammform *Odontomachus haematoda* L. ist von Wheeler abgebildet worden."

*Odontomachus affinis* Guérin.—Borgmeier, 1920, p. 37: "Nur finden sich auf dem Tuberkel nicht mehr als 5 Härchen, die jedoch viel länger sind als bei *O. haematodes* und ungefähr bis zur Spitze des Dornes reichen, der aus der Mitte des Tuberkels hervorragt." "Für *O. haematodes* hat Wheeler nachgewiesen, dass sie ihre Larven mit Fleischnahrung füttert. Für *O. affinis* ist mir kein derartigen Fall bekannt. In den ersten 3 Monaten, in denen ich den Ameisen ausschliesslich Honig und Zuckerwasser reichte, wurden die Larven gefüttert wie die aller anderen Ameisen: durch Einpumpen der Nahrung. Aber auch hernach, als ich ihnen Termiten zu fressen gab, konnte ich keinen Fall beobachten, wie ihn Wheeler beschreibt."

Wheeler, 1933, p. 15: "Since 1900 I have found so many Ponerine ant-larvae feeding on pieces of insects that Father Borgmeier's (1920) negative observations on the Brazilian *Odontomachus affinis* are somewhat surprising. Though he fed his colonies on termites as well as honey and sugar-water, he was unable to detect any other method of feeding the larvae than by regurgitation."

*Odontomachus biolleyi* Forel.—Similar to *haematoda* but differing in the following details: all hairs shorter; tubercles shorter; anterior surface of median notch of labrum with a few scattered spinules; mandibles beset with fewer rows of fewer and finer spinules; apex of maxillae dilated and lobose. (Material studied: three semipupae from Costa Rica.)

*Odontomachus chelifer* (Latreille).—Similar to *haematoda* but differing in the following details: all hairs longer; hairs on tubercles more numerous (7-14). Tubercles taller. Integumentary spinules on the dorsal surface in short rows which are arranged in a concentric pattern around tubercles and spiracles; elsewhere in transverse rows. Six hairs on clypeus. Apex of maxillae dilated and lobose. (Material studied: a larva and a semipupa from Panama Canal Zone.)

*Odontomachus rixosus* F. Smith.—Similar to *haematoda* but differing as follows: Tubercles taller and less numerous (94) due to the lack of atypical tubercles on the abdomen; basal hairs more numerous (5-10). The rows of integumentary spinules are transverse on the ventral surface of the thorax; elsewhere they form a reticulate pattern. Six hairs on the clypeus. (Material studied: five integuments from Siam.)

*Odontomachus ruficeps coriaria* Mayr.—Dodd (1906, p. 123) records

*Rhipipallus affinis* Bingham "bred from the pupae" of this ant. Presumably the eucharid larvae were parasitoid on the ant larvae.

*Odontomachus tyrannicus* F. Smith.—Similar to *haematoda,* except in the following characters: All hairs longer. Tubercles less numerous (98); atypical abdominal tubercles lacking. No dorsal paired structures on the fourth and fifth abdominal somites; in place of each is a typical tubercle. Basal hairs of tubercles more numerous (5-9). Integumentary spinules on the dorsal surface in short rows which are arranged in a concentric pattern around tubercles and spiracles; elsewhere in transverse rows. No integumentary spinules on galea. (Material studied: eight larvae and four semipupae from Dutch New Guinea.)

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## Subfamily PONERINAE Lepeletier

Shaped somewhat like a crook-neck squash; thorax and one or two abdominal somites forming a distinct neck which is curved or bent ventrally; rest of abdomen stout and straight, its ventral profile straight, its dorsal convex; ventral surface more or less flattened; usually with a longitudinal welt along each side. Posterior end rounded. Anus ventral or subterminal. Segmentation distinct, but often less so posteriorly; 7-13 differentiated somites, the majority showing 13. Leg vestiges present. Integument diverse—from smooth to densely spinulose; at least the ventral surface of the thorax is nearly always spinulose. Body furnished with either an abundant covering of hairs or with tubercles; in tuberculate larvae the hairs are few and most of them are on the tubercles. In hairy larvae the anterior portion of the prothorax is naked. Hairs typically simple, slightly curved, minute to short; straight, lash-like, denticulate or branched hairs occur in certain genera. Head on the anterior end of the body. Head shape varied. Antennae diverse in size and shape; each with three sensilla. Head hairs never numerous; minute to short; nearly always simple and slightly curved. Labrum mostly medium-sized to large, rarely small; short, breadth greater than length (mostly $1\frac{1}{2}$-2X); usually bilobed due to a median incision of the ventral border; anterior surface furnished with sensilla and minute hairs; posterior surface provided with sensilla and densely spinulose, the spinules usually minute and arranged in rows which form characteristic patterns. Mandibles large for ant larvae; moderately to heavily sclerotized; somewhat broad to slender, mostly rather narrow, curvature usually rather slight; shape diverse; typically with a single apical tooth, which is curved medially, and two prominent subapical teeth on the mesal face; in most genera the surface is more or less spinulose. Maxillae prominent; apex paraboloidal or conoidal, and spinulose; palp and galea conspicuous, slender and paxilliform. Labium prominent, spinulose; palp conspicuous, slender and paxilliform; opening of sericteries wide and salient. Hypopharynx spinulose. Trophorinium elaborate. Carnivorous, feeding typically on insect prey provided by the workers. Active. Neck flexible and used in feeding, defense and limited locomotion.

## LITERATURE ON THE SUBFAMILY

*References on Feeding.*—Bischoff, 1927, p. 87: "Bei den tiefstehenden Ponerinen werden den Larven tote Insekten und zerkautes Futter vorgelegt. Mit ihren verhältnismässig kräftigen, beweglich Mandibeln können sie diese Nahrung selbständig zu sich nehmen. Futter aus dem Kropf der Arbeiterinnen erhalten diese Larven im Gegensatz zu denen der anderen Unterfamilien der Ameisen nicht."

Brun, 1924, p. 95: "Seltener werden grösseren Larven auch mit Speichel durchtränkte Stücke erbeuteter Insekten . . . direkt zum Frasse vorgelegt. Bei den Ponerinen bildet nach den Beobachtungen Forels und Wheelers die einfachere und ursprüngliche Fütterungsart die Regel; daher sehen wir denn auch die Ponerinenlarven mit wesentlich kräftigeren Kieferstummeln ausgerustet. So verraten die Ponerinen auch in dieser Hinsicht, wie in so manchen andern biologischen Eigentümlichkeiten, noch sehr deutlich in Verharren auf verhältnismässig primitiver Entwicklungsstufe, eine Einfachheit der sozialen Sitten, die, im Verein mit einem gewissen Archaismus ihres morphologischen Gepräges, Forel mit Recht veranlasste, sie an den Anfang der phylogenetischen Entwicklungsreihe der Ameisenfamilie zu stellen."

Creighton, 1950, p. 29: "The workers collect other insects or small arthropods and these are cut to pieces and fed directly to the larvae. Regurgitation seems to play a much smaller part in the life of the colony than is the case in the higher subfamilies."

Forel, 1921a, pp. 23-24: "Wheeler surtout a bien montré que les ☿ ne leur dégorgent pas le contenu de leur propre jabot, mais qu'elles se contentent de déposer à côté d'elles des insectes morts ou autre pâtée que les larves savent ensuite dévorer seules-mêmes." (= vol. I, p. 24: "Wheeler in particular has shown that ☿ do not regurgitate the contents of their own crops to the larvae, but that they merely place beside them dead insects or other food which the larvae can afterwards eat on their own account."

Forel, 1921a, p. 134: "Elles nourrissent leurs larves directement en leur apportant des morceaux d'insectes ou de quelque autre comestible, que celles-ci doivent ronger elles-mêmes. Les *Ponerinae* donnent donc habituellement à manger aux larves, par un procédé plus primitif, qui est exceptionnel chez les autres fourmis. Les larves des *Ponerinae* ont une mobilité extraordinaire pour des larves de fourmis. Quand elles sont inquiétées, elles agitent leur long cou comme pour se défendre. Beaucoup d'entre elles ont des tubercules sur la peau." (= 1928, vol. I, p. 129: "They feed their larvae directly by bringing them pieces of insects or some other food, which the larvae have to gnaw for themselves. The *Ponerinae* therefore supply food direct to their larvae by a more primitive process, exceptional among the other ants. The larvae of the *Ponerinae* are remarkably mobile for ant-larvae. When they are disturbed, they move their long necks as though trying to defend themselves. Many of them have tubercles on the skin.")

Forel, 1922, p. 136: "Les larves des *Ponerinae* . . . se nourrissent des proies entières ou decoupées que leur donnent les ☿ sans les emboquer; elles sont assez mobiles et indépendantes pour manger seules." (= 1928, Vol. I, p.

516: "The larvae of the *Ponerinae* . . . feed on prey, whole or in fragments, which the ☿ supply to them without cramming. . . . They are sufficiently mobile and independent to eat alone.")

Forel, 1923, p. 116: "Wheeler a bien prouvé qu'elle dévore seule les proies mortes ou inertes que les ☿ ou les ♀ mettent à sa disposition. Cela paraît être le cas chez tous les *Ponerinae*." (= 1928, vol. II, p. 298: "Wheeler has actually proved that it devours unaided the dead or motionless prey which the ☿ or ♀ place at its disposal. This seems to be the case with all the *Ponerinae*."

Kellogg, 1905, pp. 540-541: a good abstract of Wheeler, 1900a, pp. 26-28.

Krausse, 1929, pp. 96-97: "Meist sind sie nur imstande flüssige Nahrung, die ihnen die Arbeiterinnen reichen, aufzunehmen. Doch können die Larven der Ponerinen und anderer Arten auch feste Nahrung, zerstückelte Insekten usw., selbständig fressen."

Wheeler, 1900a, pp. 26-28: "These observations lead us to several interesting reflections. First, it is certain that the feeding of the larva of the Ponerinae is of a far more primitive character than in any other ants in which this process has been studied. It is, in fact, even more primitive than the corresponding habit of the social wasps, which feed their larvae with masticated insect prey, for in the Ponerinae the prey is cut into a few pieces only, for the purpose of exposing the soft tissues and making them accessible to the mandibles of the larvae. Myriopods or large insects are disarticulated for this purpose, small insects are merely torn open. Leaving the question of systematic affinities out of consideration, the Ponerinae may be said to have habits of feeding the young intermediate between the habits of the solitary wasps, which provide their young with whole insects, and the social wasps, which masticate the food for their larvae. In this statement it may, perhaps, be more accurate to substitute the Bembecidae for the solitary wasps, since the Bembecidae, which feed their larvae from day to day with entire Diptera in a fresh condition, resemble the Ponerinae more closely than do the solitary wasps, which merely enclose their eggs with paralyzed larvae, spiders, grasshoppers, etc. From the condition of the Ponerinae to that of the more specialized ants, which feed their larvae with nothing but the liquid food regurgitated from their own crops or from their salivary glands, the transition is very abrupt. But there are many ants whose habits have not been studied, and some of these may yet be found to bridge this chasm.

"In the second place, the above-recorded observations seem to show that the Ponerine method of feeding the larvae is of a most capricious and irregular character. The quantity and quality of the food given to a particular larva, and the time it is permitted to feed, seem to be matters requiring no very strict regulation. The ants that feed the young rarely act in concert, but rather with a whimsical individualism that seems at times to border on the ridiculous.

"This irregular method of feeding suggests other considerations of a wider bearing. It is generally admitted that the polymorphism of the female sex in ants, *i.e.*, the occurrence of fertile females and of sterile females of one or more casts, is in some manner correlated with the feeding of the larvae developed

from fertilized eggs. In other words, the worker ants can control the production of individuals like themselves and of individuals like their queen. It is further maintained that these differences are effected by the quantity and quality of the food administered to the larvae at a certain period of their development; but here our knowledge ends. These data have been accumulated from the study of the specialized Myrmicine and Formicine ants of Europe and North America, and are supported by many valuable observations on the hive-bee. Now, while we can, perhaps, understand how these more specialized ants may manage to control the quantity and quality of liquid food regurgitated from their own crops and salivary glands, it is not so easy to understand how ants can exercise such control when they adopt a capricious method of feeding like that of the Ponerinae. Such a method can hardly produce clear-cut results; *i.e.*, either workers or fertile females. And a comparative study of the better known species of Ponerinae shows that in certain species at least there is no such sharp distinction between the sterile and fertile female as we find in the more specialized ants."

Wheeler, 1910, p. 234: "All Ponerine larvae, so far as observed, are fed with pieces of insect food. This method, which is undoubtedly very primitive, is also adopted by many specialized ants, but as a rule their larvae are given regurgitated food."

Wheeler, 1918, p. 299: In our North American Ponerinae the larva is "placed on its back by the nurses and fed with fragments of insects deposited on its trough-like ventral surface."

Wheeler, 1922, p. 56: "In the Ponerinae the larvae are nearly always fed with pieces of solid food, which is almost invariably animal matter."

*References on Anatomy.*—(Emery 1899, p. 8) describes the ponerine type of ant larvae: "con le mandibole robuste e sporgenti e con le appendici piligere dei segmenti del loro tronco."

Emery (1904b) describes the larvae of the Ponerinae as "piriformi o claviformi, con l'addome fortemente rigonfiato, tanto in quelle che portano soltanto peli semplici, come le larve di *Stigmatomma, e Ectatomma,* alle quali aggiungerò quella ancora inedita di *Mystrium,* quanto in quelle che sono fornite di tubercoli piligeri" (pp. 114-115). On page 115 he refers to "la forma tozza e panciuta delle larve di Ponerinae." On page 116 he divides the ponerine larvae into "due gruppi principali: nell'uno di essi che considero come relativamente primitivo, . . . le larve . . . non hanno tubercoli piligeri; comprende le tribù dei Myrmecii, Amblyoponii, Ectatommii, Proceratii e Platythyrei. Nell'altro gruppo, . . . le larve sono tubercolate; comprende tutte le Ponerinae non riferibili al gruppo precedente."

Emery, *Genera Insectorum,* 1911, p. 3: "Les larves des Ponérines ont une mobilité extraordinaire pour des larves de Fourmis. Quand elles sont inquiétées, elles agitent leur long cou comme pour se défendre." In the key to sections (p. 4), he employs larval (as well as adult) characters: "Proponerinae.—Larves uniformément poilues, sans tubercules piligères. . . . Euponerinae. —Larves pourvues de tubercules piligères." Later (p. 16) in characterizing the section Proponerinae: "Larve uniformément poilue, sans tubercules pili-

gères; les segments antérieurs formant un cou plus ou moins grêle, porté sur les segments abdominaux ventrus." For the section Euponerinae: "Larve hérissée de pointes ou de tubercules régulièrement disposés en séries transversales sur chaque segment, portant des poils isolés ou en couronne, d'un aspect tout à fait caractéristique. Ces larves ont un cou grêle" (p. 53).

Escherich, 1917, p. 95: "Bei den Larven der Ponerinen finden wir auf der Oberfläche in regelmässiger segmentaler Anordnung grosse Warzen oder Papillen, welche ihrerseits mit Stacheln, Borsten und kleine Zähnchen besetzt sind."

Forel, 1923, p. 116: "Nous avons vu . . . l'image de leurs larves mobiles, fort indépendantes, pourvues d'une bouche à bonnes mâchoires. Comparée à celles des autres sous-familles . . . elle a presque l'air d'une bête féroce auprès d'enfants au maillot." (= 1928, vol. II, p. 298: "Fig. 1A is an illustration of their mobile larvae, which are very independent and have mouths supplied with serviceable jaws. Compared with those of the other sub-families . . . it looks almost like some fierce animal by the side of children in swaddling-clothes.")

Wheeler, 1910, p. 233: "The great differences between the various tribes of Ponerine ants are reflected in the structure of their larvae. At least three different types may be distinguished among the species that have been studied by Emery . . . and myself . . .: 1. Smooth, thickset larvae, with short, sparse hairs and peculiar unpaired tubercles on the midventral surface of some of the abdominal segments (*Platythyrea*). 2. Smooth, slender larvae, with a rather dense covering of hairs (*Myrmecia, Stigmatomma, Parasyscia, Ectatomma*). 3. Larvae furnished with rows of tubercles which may be pointed or boss-like, tipped or merely encircled with stout hairs (*Pachycondyla, Ponera, Pseudoponera* [*Euponera*], *Leptogenys, Diacamma, Odontomachus, Anochetus*)."

Wheeler, 1920: ". . . rudiments of antennae (which are also present in the larvae of many other ants, notably in the Ponerinae)" (p. 47). "In many ants (Ponerinae)" the trophorhinium "may be used for comminuting parts of insects given directly to the larvae by the workers. . . . Many ant-larvae, notably those of the Ectatommiine Ponerinae . . ., also have elaborate but coarser stridulatory surfaces on the mandibles, so that the larva may be able to produce a variety of sounds and therefore apprise the nurses of more than one need or craving" (pp. 48-49).

Wheeler, 1922, p. 56: "Larvae with the mandibles powerfully developed for ant larvae; the anterior portion of the body long, slender and neck-like, folded over the swollen abdominal portion; the segments are either densely hairy all over or covered with rows of peculiar tubercles beset with more or less prominent bristles; the larvae of *Megaponera* and *Bothroponera* are hairless."

## TRIBES

We have not found it feasible to characterize the tribes, chiefly because in most of them the sampling of genera is inadequate, but the following comments seem appropriate:

Tribe Cylindromyrmicini. Not represented in our collection.

Tribe Myrmeciini. We have one (Myrmecia) of the two genera, but it includes nearly all of the known species.

Tribe Amblyoponini. We have three of the six genera. Not sufficiently homogeneous to define.

Tribe Paraponerini. Only one genus.

Tribe Platythyreini. Only one genus.

Tribe Ectatommini. We have eight of the 15 genera. If Prionopelta is excluded, we can characterize the known genera by two traits: antennae small but projecting conspicuously from the head; their diameter not greater than their length; each bears three apical sensilla, each of which is surmounted by a conspicuous stout spinule; body hairs branched or at least denticulate.

Tribe Thaumatomyrmicini. Not represented.

Tribe Proceratiini. We have only one of the eight genera. The larvae of this one (Proceratium) are scarcely recognizable as ant larvae.

Tribe Dorylozelini. Not represented.

Tribe Ponerini. We have 12 of the 33 genera. If Megaponera is excluded, we can characterize the known larvae by only two traits: body furnished with tubercles whic are not smoothly rounded bosses and are not restricted to the ventral surfaces; body hairs (other than those on tubercles) usually very few and small.

Tribe Onychomyrmicini. Only one genus (Onychomyrmex). As stated above, this genus shows more affinities with the Cerapachyinae than with the Ponerinae.

Tribe Leptogenyini. We have one (Leptogenys) of the two genera, but it includes nearly all of the known species.

Tribe Odontomachini. We have two of the four genera, but since these two include nearly all the known species, we feel justified in defining this tribe: Neck long and somewhat stout; abdomen straight and rather stout. Tubercles moderately numerous (92-112); the majority consisting of a subconical base bearing 3-14 relatively long hairs; on this base is seated a much slender cone, which has mounted on its apex a heavy straight spine-like hair; integument of distal cone with short transverse rows of spinules. On the middorsal surface of abdominal somite IV there is one or a pair of glabrous areas which may be almost flush or noticeably elevated; similar areas on V.

## Genera

In contrast to this tribal complexity stands the simplicity of the generic situation. Most genera may be readily defined by an adequate number of clear-cut characters. Among these characters are one or more which facilitate identification. In other words, it is easy to construct a key.

Nevertheless there are two groups of genera which constitute exceptions:

1. Emeryella, Stictoponera, Ectatomma (Poneracantha), E. (Parectatomma), E. (Gnamptogenys) are so similar that they can be separated only by differences of a sort that distinguish species elsewhere. It is interesting to note that Emery in the *Genera Insectorum* regarded Emeryella as very close to Gnamptogenys.

2. Rhytidoponera and Chalcoponera are likewise difficult to separate and characterize. In the *Genera Insectorum* they are both subgenera of the genus Rhytidoponera.

KEY TO THE GENERA OF MATURE PONERINE LARVAE IN OUR COLLECTION

1. Body without tubercles ........ 2
   Body beset with tubercles ........ 18
2. Body apparently naked (hairs about 0.009 mm long) ........ *Megaponera*
   Body hairs easily seen ........ 3
3. Branched or denticulate body hairs present ........ 4
   Body hairs all simple ........ 13
4. Head hairs denticulate; body hairs whip-like, with the base denticulate ........ *Ectatomma* (*Ectatomma*)
   Not as above ........ 5
5. Head hairs simple ........ 6
   Head hairs branched ........ 12
6. Mandibles with all spinules short ........ 7
   Mandibles with some of the spinules longer and grouped in prominent combs ........ 8
7. Mandibles with a deep and wide notch between the two medial teeth; apical tooth straight ........ *Rhytidoponera*
   Mandibles with a deep but narrow notch between the two medial teeth, apical tooth curved, narrow and sharp pointed ........ *Chalcoponera*
8. Body hairs all with long branches ........ *Stictoponera*
   Some body hairs with short branches (denticles) ........ 9
9. Mandibles with all teeth blunt ........ *Emeryella*
   Mandibles with the medial teeth acute ........ 10
10. Body hairs all with short lateral branches ........ *Ectatomma* (*Poneracantha*)
    Most body hairs with long branches ........ 11
11. Antennae about as long as their diameter; body hairs mostly bifid ........ *Ectatomma* (*Parectatomma*)
    Antennae about twice as long as their diameter; body hairs mostly 4-branched ........ *Ectatomma* (*Gnamptogenys*)
12. Mandibles with some of the spinules longer and grouped in prominent combs ........ *Holcoponera*
    Mandibles with all spinules minute; mandible divided into a greatly inflated base and a very slender distal portion ........ *Typhlomyrmex*
13. Not distinctly differentiated into a more slender "neck" and a stouter "body" ........ 14
    Differentiated into a more slender "neck" and a stouter "body" ........ 16
14. Diameter least at the first abdominal somite; thorax swollen ........ *Onychomyrmex*
    Not as above ........ 15
15. Hairs all short and slightly curved ........ *Myrmecia*
    Most hairs short, but some much longer and lash-like ........ *Prionopelta*
16. Mandibles with teeth on the anterior surface as well as the medial surface ........ *Stigmatomma*
    Mandibles with teeth on the medial surface only ........ 17
17. Mandibles very narrow and elongate; body sparsely hairy ........ *Amblyopone*
    Mandibles broad and subtriangular; body densely hairy ........ *Paraponera*
18. Tubercles few (less than 50) and inconspicuous, restricted either to the ventral or to the lateral surfaces ........ 19
    Tubercles numerous (80 to 400) and conspicuous ........ 20
19. Tubercles restricted to ventral surface ........ *Platythyrea*
    Tubercles lateral ........ *Bothroponera*
20. Tubercles of two distinct types; mostly finger-like; a few pairs of conspicuous doorknob-shaped tubercles on the dorsal surface ........ 21
    Tubercles not as above ........ 23
21. Hairs denticulate ........ *Cryptopone*
    Hairs simple ........ 22

22. Finger-like tubercles with a conspicuous apical spine-like hair ........ *Ponera*
Finger-like tubercles without apical spine ........ *Euponera* (*Trachymesopus*) *gilva*
23. Tubercles consisting of a subconical base bearing relatively long hairs and surmounted by a slender spinulose cone which bears on its apex a conspicuous spine-like hair (Tribe Odontomachini) ........ 24
Tubercles not as above ........ 27
24. With glabrous areas, partially fringed by hairs, on the dorsum of abdominal somites IV and V ........ 25
Without such areas on the dorsum ........ *Odontomachus tyrannicus*
25. A single glabrous area on the dorsum of each of abdominal somites IV and V ........ *Anochetus* (*Anochetus*)
A pair of glabrous areas on the dorsum of each of abdominal somites IV and V .. 26
26. Mandibles with medial teeth subequal to the apical tooth ........ *Odontomachus* (except *O. tyrannicus*)
Mandibles with medial teeth reduced to denticles ........ *Anochetus* (*Stenomyrmex*)
27. Body beset with numerous rounded (but not mammiform) tubercles which are generally distributed (even on the dorsal surface); mandibles reduced and without teeth ........ *Proceratium*
Tubercles not as above; mandibles well developed ........ 28
28. Tubercles mammiform ........ 29
Tubercles not mammiform ........ 31
29. Mandibles with a posterior denticle but without medial teeth; labrum narrow, not bilobed ........ *Leptogenys*
Mandibles with distinct medial teeth; labrum broad and bilobed ........ 30
30. Mandibles with two apical and one subapical tooth; cranium short (a third broader than long) ........ *Dinoponera*
Mandibles with one apical and two subapical teeth; cranium as broad as long ........ *Pachycondyla*
31. Tubercles very numerous (350-400) and so slender as to simulate hairs ........ *Centromyrmex*
Tubercles less numerous (not over 200); not hair-like ........ 32
32. Tubercles subconical ........ 33
Tubercles not subconical ........ 36
33. Tubercles with spinules confined to apex ........ *Trapeziopelta*
Tubercles encircled by rows of spinules ........ 34
34. Tubercles with several lateral hairs; head hairs minute and inconspicuous ....*Neoponera*
Tubercles with minute apical (but no lateral) hairs; head hairs short but conspicuous ........ 35
35. Tubercles attenuated to a slender spire ........ *Odontoponera*
Tubercles not as above ........ *Euponera* (*Mesoponera*) *constricta* and *E.* (*Trachymesopus*) *stigma*
36. Tubercles paraboloidal, crowned with minute conoidal papilla ........ *Diacamma australe*
Tubercles consisting of an expanded base and a distal spine-like projection ........ *Diacamma scalpratum* and *D. rugosum* subspp

## SPECIES

Concerning specific differences no general statement can be made. Thirteen of our genera are represented by only one species each. The others may be grouped according to the degree of differentiation of the species in our collection:

1. Species indistinguishable—Holcoponera, Chalcoponera, Ectatomma (*s. str.*).

2. Species scarcely distinguishable.—Myrmecia, Amblyopone, Stictoponera, Rhytidoponera, Proceratium, Pachycondyla.

3. Species easily distinguishable.—Ectatomma (*s. lat.*), Diacamma, Neoponera, Bothroponera, Euponera, Ponera, Trapeziopelta, Leptogenys, Anochetus, Odontomachus.

4. Specific differences of generic magnitude.—*Diacamma australe* vs. *D. rugosum* and *D. scalpratum*—on account of tubercles. The genus Ectatomma (*s. lat.*) presents a peculiar situation: subgenus Ectatomma vs. subgenera Poneracantha, Parectatomma and Gnamptogenys—on account of body hairs, antennae, shape of mandibles and mandibular spinules; in fact the last three subgenera more closely resemble the genus Emeryella than their congeneric subgenus Ectatomma. A similar situation obtains in the genus Anochetus: subgenus Anochetus vs. subgenus Stenomyrmex—on account of the labrum, mandibles and peculiar glabrous areas on the dorsa of abdominal somites IV and V; in fact the larvae of Anochetus *s. str.* are more like those of the genus Odontomachus than their own congeners of the subgenus Stenomyrmex. The situation in Euponera, which is considerably more complicated, is discussed above under the genus.

## Discussion

The larvae of the Ponerinae do not constitute as homogeneous a group as do the Dorylinae or the Cerapachyinae or the Attini, but this is perhaps to be expected since they are a much larger group. The nearest to a distinctive character is probably body shape; yet a fourth of the larvae studied are exceptional in this respect. We cannot select any one genus and call it typical; Centromyrmex may be as close as any. Certain genera are so aberrant that they can hardly be recognized as ponerines: Platythyrea, Prionopelta, Proceratiam, Megaponera and Onychomyrmex. Prionopelta, Megaponera and Onychomyrmex are more like dorylines or cerapachyines. Platythyrea and Proceratium are *sui generis*.

Among the typical ponerine larvae the most specialized of the nontuberculate genera occur in the tribe Ectatommini; among the tuberculate genera it is possibly Leptogenys.

Wheeler (1918, p. 295) considered the adults of *Myrmecia sanguinea* to be the most primitive of existing Formicidae. We believe that the same can be said of the larva, which we regard as primitive in every respect, but notably in the following details: body shape; short, simple and abundant hairs; few minute hairs on the head; size, shape and position of antennae; general size and shape of labrum; posterior labral spinules are not in rows but isolated; palp and galea peg-like and only moderately long; labial palp a low rounded elevation; opening of sericteries wide but not salient.

Other genera which are primitive—both in adult and larval stages—are Stigmatomma, Amblyopone, Mystrium and Paraponera. The first two show some advance in body shape in mandibles and in longer hairs. The larva of Paraponera is almost as primitive as that of Myrmecia; its body shape, however, is ponerine. Mosley (Bull. Soc. Ent. France 43: 190-194, 6 figs. 1938.) regards Mystrium as the possible ancestor of all Formicidae. It is most unfortunate, therefore, that our single larva is in such poor condition. From those

parts available, however, we judge it to be somewhat less primitive than Myrmecia.

It seems to us that the following phylogenetic hypothesis might be justified: The larva of Myrmecia represents the ancestral formicid type from which the higher ponerine larvae evolved by differentiation into a slender curved "neck" and larger "body." Before this differentiation occurred, a side branch was formed, the larvae of which became more attenuated posteriorly; this line led to the Cerapachyinae. A secondary offshoot from it gave rise through a straightening of the larval body to the Dorylinae.

## SUMMARY

The larvae of 67 species in 31 genera are described and illustrated. References to ponerine larvae from the literature are cited, bringing the total number of species and genera considered up to 93 and 32 respectively. A bibliography is appended. The larvae of the Ponerinae do not constitute a homogeneous group and consequently are difficult to characterize as a subfamily. Most tribes cannot be characterized at present. Genera, on the other hand, are easy to distinguish and define. A key to the genera is included. Within genera, however, larval taxonomy is not closely correlated with adult taxonomy: in some genera the species show differences of generic magnitude; in others the differences are less striking, but the species are easily separated; in some the species are difficult to distinguish, while in a few they are indistinguishable. By way of contrast, a phylogenetic tree based on larval characters would be similar to that based on adult characters: Myrmecia is regarded as the most primitive and putatively ancestral to the Ponerinae (and in fact to all Formicidae); two lines of evolution culminate in the Ectatommini and in the Leptogenyini.

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## EXPLANATION OF PLATES

PLATE I. *Centromyrmex feae* Emery, Figs. 1-10.—1, head in anterior view, ×56; 2, right half of labrum in posterior view, ×118; 3, body hair, ×121; 4, larva in side view, ×12; 5, right mandible in anterior view, ×121; 6, right mandible in posterior view, ×121; 7-10, four body tubercles, ×121.

*Odontoponera transversa* (F. Smith), Figs. 11-19.—11, head in anterior view, ×44; 12, integument of body, ×117; 13, left mandible in anterior view, ×60; 14, tubercle, ×117; 15, head hair, ×185; 16, larva in side view, ×10; 17, spinules of head in surface view, ×185; 18, spinules of head in profile, ×185; 19, ventrolateral organ of abdominal somite V, ×117.

*Megaponera foetens* (Fabricius), Figs. 20-25.—20, head in anterior view, ×22; 21, left mandible in anterior view, ×44; 22, body hair, ×370; 23, metathoracic leg vestiges in surface view, ×44; 24, lateral third of abdominal somite III in ventral view, ×22; 25, larva in side view, ×4.

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*Diacamma australe* (Fabricius), Figs. 9-18.—9, head in anterior view, ×33; 10, left mandible in anterior view, ×73; 11, tubercle, ×92; 12, larva in side view, ×8; 13, integumentary pattern on gula, ×183; 14, integumentary pattern on cranium, ×183; 15, left galea in anterior view, ×95; 16, body hair, ×100; 17, body spinules in profile, ×185; 18, structure near spiracle on abdominal somite III, ×47.

*Diacamma scalpratum* (F. Smith), Figs. 19 and 20.—19, body hair, ×100; 20, tubercle, ×92.

*Diacamma rugosum viridipurpureum* Emery, Figs. 21-24.—21, body hair, ×100; 22, tubercle, ×100; 23, labium of young in anterior view, ×40; 24, labium of young in side view enclosing labium of next instar larva, ×40.

*Bothroponera* sp., Fig. 25, head in anterior view, ×44.

*Bothroponera sublaevis* Emery, Figs. 26-30.—26, left mandible in posterior view, ×47; 27, tubercle, ×92; 28, left metathoracic leg vestige and spinules, ×44; 29, body spinules in profile, ×185; 30, body hair, ×185.

PLATE III. *Pachycondyla striata* F. Smith, Figs. 1-10.—1, head in anterior view, ×28; 2, labrum in posterior view (right half only), ×61; 3, larva in side view, ×7; 4, right mandible in anterior view, ×61; 5, body hair, ×185; 6, tubercle hair, ×185; 7, immature tubercle enclosing mature tubercle, ×121; 8, mature tubercle in side view, ×57; 9, mature tubercle in surface view, ×57; 10, young larva in ventral view, ×7.

*Neoponera villosa* (Fabricius), Figs. 11, 12, 14 and 18.—11, abdominal tubercle, ×47; 12, thoracic tubercle, ×47; 14, right mandible in anterior view, ×47; 18, head in anterior view, ×32.

*Neoponera apicalis* (Latreille), Fig. 13, thoracic tubercle, ×47.

*Neoponera obscuricornis latreillei* Forel, Figs. 15-17 and 19.—15, integumentary spinules and body hair, ×185; 16, mature vestigial abdominal tubercle, ×47; 17, thoracic tubercle, ×47; 19, immature larva in side view, ×10.

*Cryptopone mayri* Mann, Figs. 20-26.—20, head in anterior view, ×80; 21, dorsal abdominal tubercle, ×108; 22, galea, ×233; 23, maxillary palp, ×233; 24, tubercle, ×167; 25, body hair, ×167; 26, left mandible in anterior view, ×185.

PLATE IV. *Euponera* (*Mesoponera*) *constricta* (Mayr), Figs. 1-7.—1, head in anterior view, ×33; 2, left mandible in anterior view, ×92; 3, larva in side view, ×13; 4, thoracic tubercle, ×106; 5, body hair, ×185; 6, abdominal tubercle, ×106; 7, dorsal abdominal tubercle, ×106.

*Euponera* (*Trachymesopus*) *gilva* (Roger), Figs. 8-16.—8, left maxilla in anterior view, ×118; 9, labrum in posterior view (right half only), ×118; 10, right mandible in anterior view, ×118; 11, head in anterior view, ×71; 12, labium and hypopharynx in side view, ×118; 13, body hair, ×125; 14, abdominal tubercle, ×119; 15, doorknob-shaped tubercle, ×137; 16, larva in side view, ×15.

*Trapeziopelta* sp. (labelled "British N. Borneo E. Mjöberg), Figs. 17-31.—17, head in anterior view, ×44; 18, right mandible in anterior view, ×95; 19, right mandible in medial view, ×95; 20, left maxilla in anterior view, ×95; 21, left maxillary palp in ventral view, ×185; 22, left labial palp in anterior view, ×185; 23, dorsolateral integumentary structure, ×38; 24, two body hairs, ×191; 25, larva in side view, ×8; 26, labrum in posterior view, ×92; 27, a labral comb, ×333; 28, typical abdominal tubercle, ×44; 29, dorsal abdominal tubercle, ×44; 30, dorsal thoracic tubercle, ×44; 31, lateral thoracic tubercle, ×44.

PLATE V. *Anochetus* (*Anochetus*) sp. (labelled "Tobang Borneo 1300 m E. Mjöberg"), Figs. 1-11.—1, head in anterior view, ×47; 2, left antenna in side view, ×185; 3, typical tubercle, ×67; 4, left mandible in anterior view, ×73; 5 and 7, two body hairs, ×185; 6, ventrolateral thoracic tubercle, ×67; 8, larva in side view, ×11; 9, pattern and spinules of integument, ×130; 10, "pulley" on dorsum of abdominal somite IV or V, in side view, ×33; 11; "pulley" on dorsum of abdominal somite IV or V, in dorsal view, ×33.

*Anochetus* (*Stenomyrmex*) *emarginatus* (Fabricius), Figs. 12, 13 and 15-17.—12, head in anterior view, ×44; 13, right mandible in posterior view, ×92; 15, elevated area on dorsum of abdominal somite IV or V, in side view, ×33; 16, elevated area on dorsum of abdominal somite IV or V, in dorsal view, ×33; 17, body hair, ×67.

*Anochetus* (*Stenomyrmex*) *emarginatus rugosus* Emery, Fig. 14, palp and galea of left maxilla in anterior view, ×130.

*Ponera coarctata pennsylvanica* Buckley, Figs. 18-21 and 28-32.—18, head in anterior view, ×71; 19, right mandible in anterior view, ×118; 20, right mandible in posterior view, ×118; 21, larva in side view, ×19; 28, doorknob-like tubercle, ×185; 29, spire-like tubercle, ×185; 30, spinules on dorsal surface of abdomen in dorsal view and in profile, ×185; 31, spinules on ventral surface of abdomen in ventral view and in profile, ×185; 32, two body hairs, ×185.

*Ponera* sp. (North Dakota, greenhouse, No. 417), Figs. 22-27.—22, spinules on dorsal surface in profile, ×185; 23, spinules on ventral surface in ventral view, ×185; 24, spire-like tubercle, ×185; 25, doorknob-like tubercle, ×185; 26, body hair, ×185; 27, ventrolateral prothoracic projection, ×185.

*Ponera* sp. (from New South Wales), Fig. 33, head, pro- and mesothorax in ventral view to show flap-like projections, ×47.

PLATE VI. *Onchomyrmex mjöbergi* Forel, Figs. 1-7.—1, head in anterior view, ×95; 2, labrum in posterior view (right half only), ×185; 3, body hair, ×180; 4, left mandible in anterior view, ×111; 5, right maxillary palp in anterior view, ×367; 6, right mandible in medial view, ×111; 7, larva in side view, ×20.

*Leptogenys (Lobopelta) elongata* (Buckley), Figs. 8-10.—8, right mandible in medial view, ×117; 9, labrum in anterior view, ×117; 10, labrum in side view, ×117.

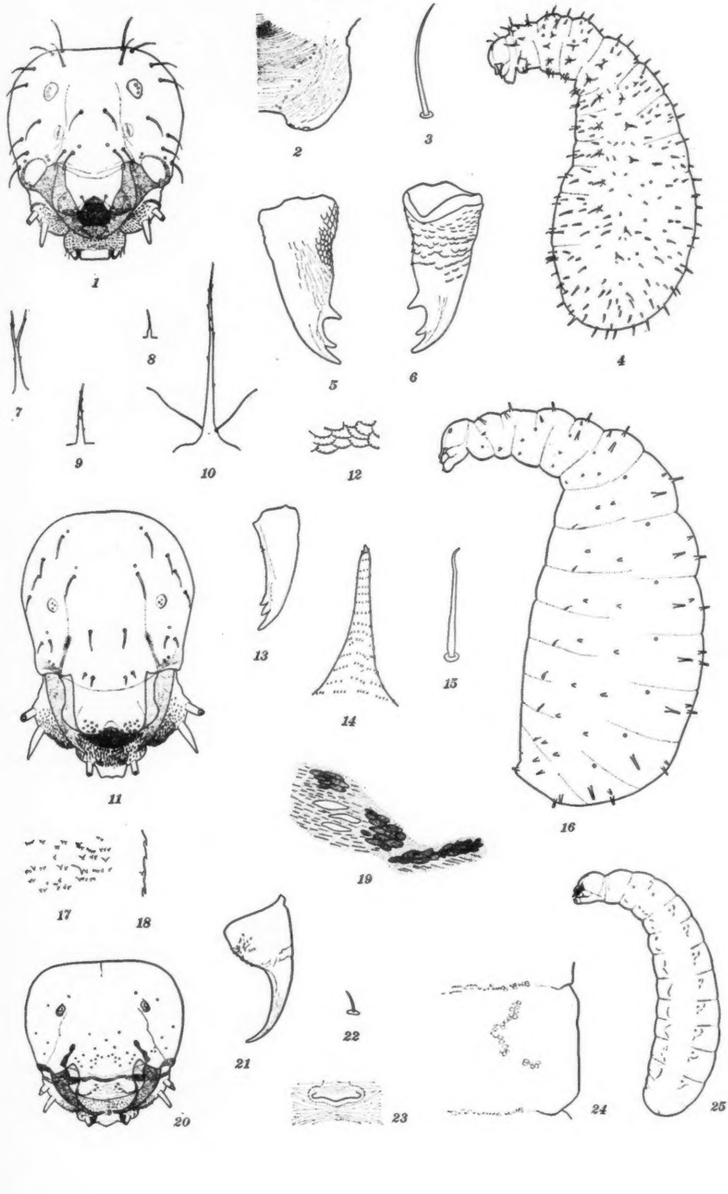
*Leptogenys (Odontopelta) turneri* Forel, Fig. 11, thoracic tubercle, ×72.

*Leptogenys (Leptogenys)* sp. (Panama Canal Zone, No. 119), Figs. 12, 13 and 15-21.—12, head in anterior view, ×77; 13, labrum in posterior view, ×117; 15, thoracic tubercle, ×72; 16, body hair, ×224; 17, abdominal tubercle, ×72; 18, right mandible in anterior view, ×117; 19, right mandible in posterior view, ×117; 20, right mandible in medial view, ×117; 21, right mandible in side view, ×117.

*Leptogenys (Leptogenys)* sp. (Panama Canal Zone, No. 43), Fig. 14, larva in side view, ×8.

*Odontomachus haematoda* (Linnaeus), Figs. 22-29.—22, head in anterior view, ×36; 23, typical tubercle, ×56; 24, atypical thoracic tubercle, ×56; 25, atypical abdominal tubercle, ×56; 26, larva in side view, ×11; 27, left mandible in anterior view, ×60; 28, body hair, ×231; 29, glabrous areas on dorsal surface of abdominal somite IV, in dorsal view, ×56.

PLATE I



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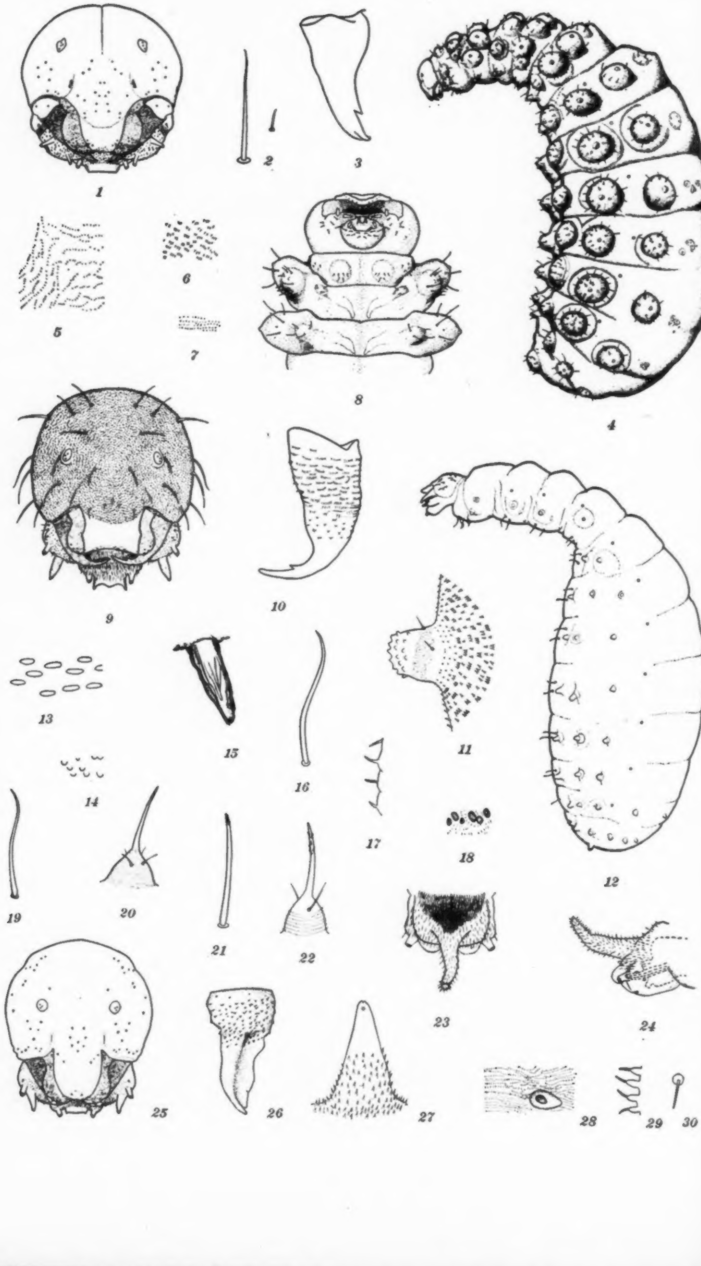
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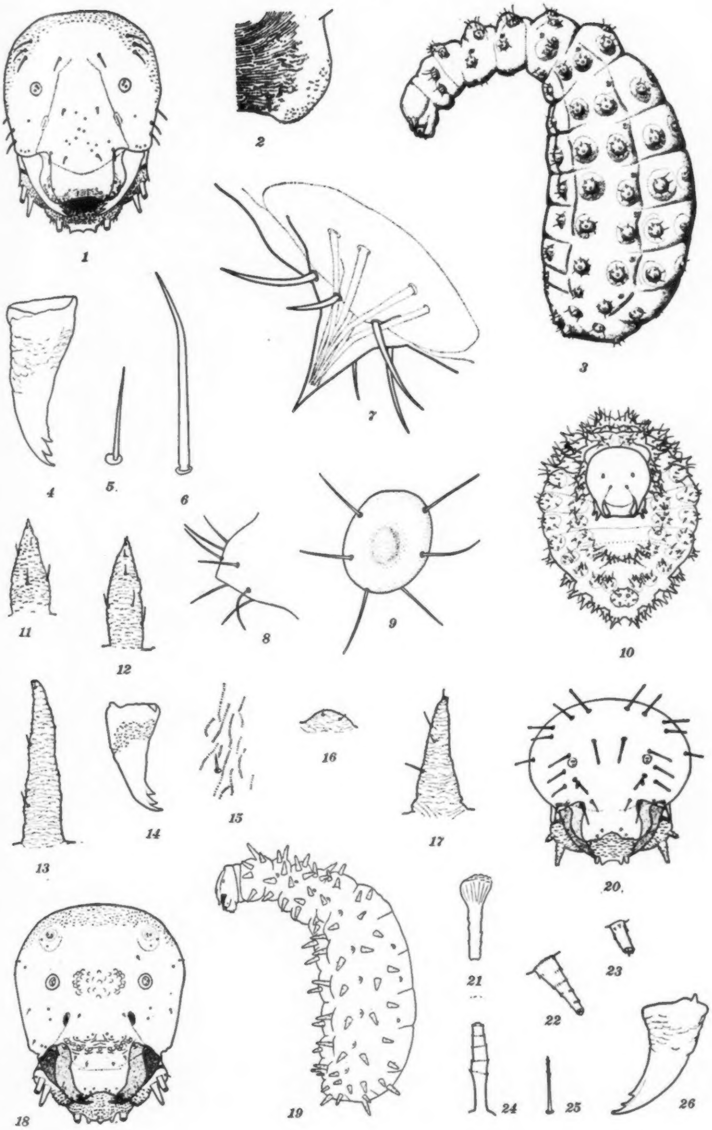
PLATE III



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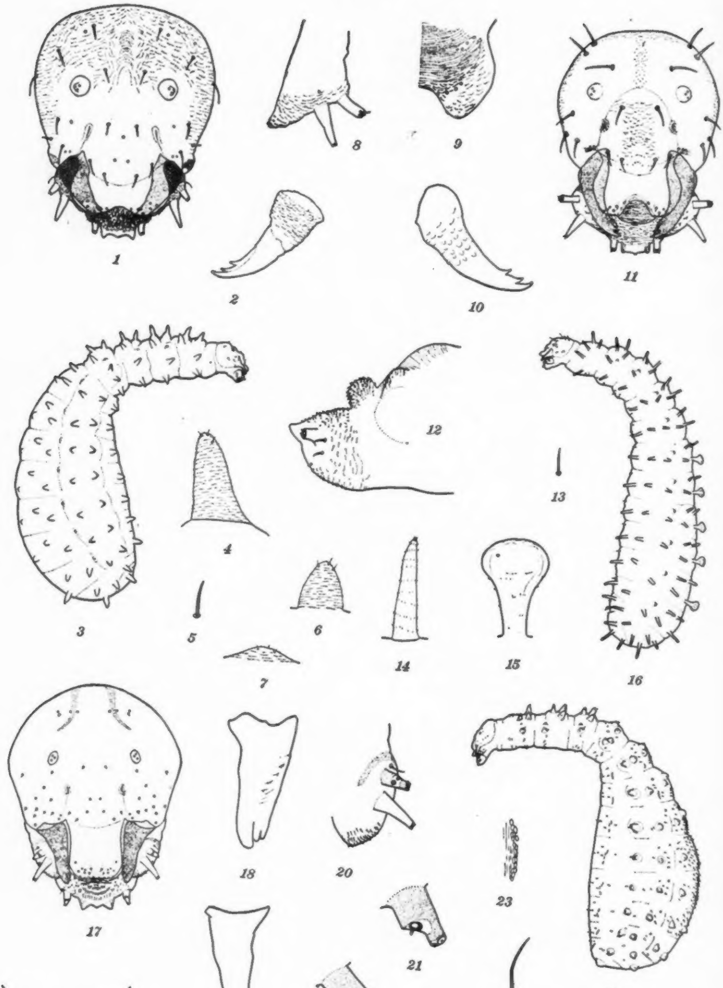
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PLATE V

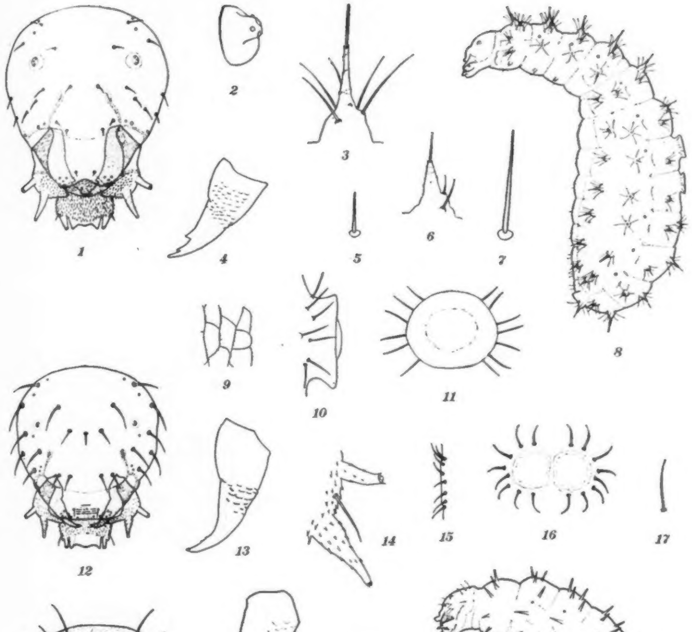
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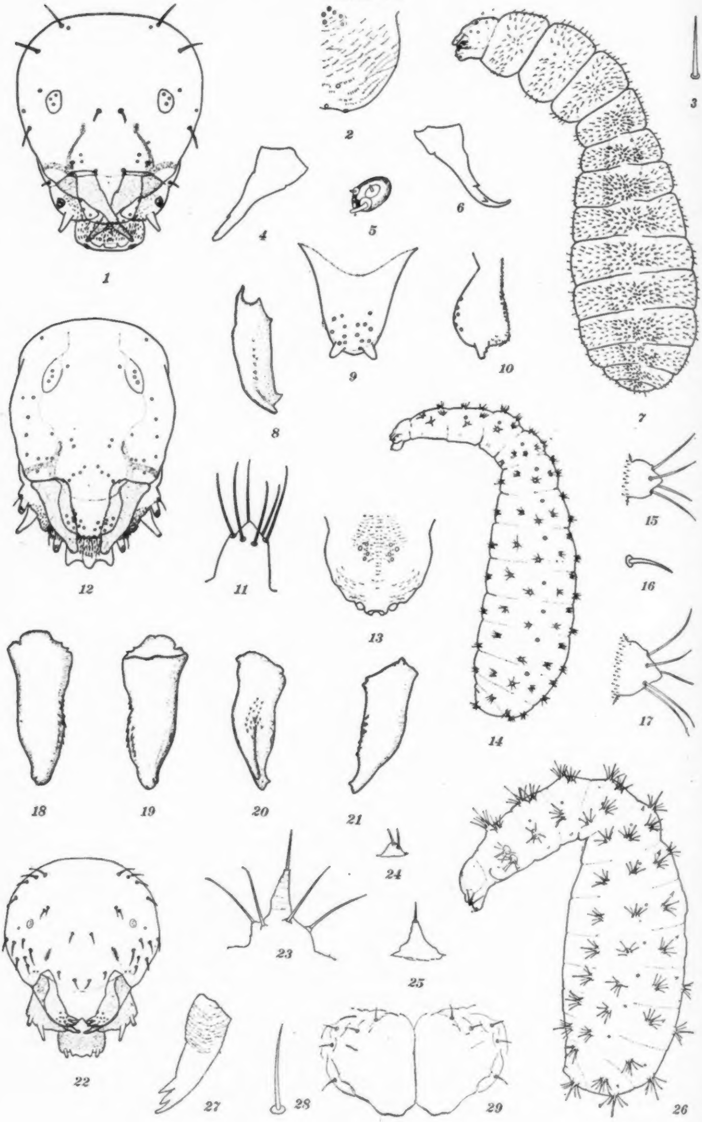
PLATE VI



# Mosquito Studies in the Panama Canal Zone During 1949 and 1950 (Diptera, Culicidae)[1]

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Mosquito control was a problem of major consideration during the construction of the Panama Canal and has since continued to receive much attention from personnel responsible for the maintenance and defense of the Canal. The accomplishments in malaria control in the Canal Zone would indeed constitute one of the brightest chapters in a history of modern preventive medicine.

At this time there is no complete work on the mosquito fauna of this vital area. Howard, Dyar and Knab (1912-1917) and Dyar (1925 and 1928) include systematic treatments of the Culicidae known for the area at the time of these publications. Since then there has been published only occasional descriptions of new species and notes, except for *The Anopheline Mosquitoes of The Caribbean Region* by Komp (1942), *Notes on Distribution and Bionomics of Panama Mosquitoes* by Arnett (1947-1950) and *Studies on Forest Mosquitoes in Panama* by Galindo *et al.*, (1949, 1950 and 1951).

This present paper includes a summary of the mosquitoes collected and identified by personnel of the 25th Preventive Medicine Survey Detachment while engaged in work on Army posts located in both the Atlantic and Pacific sectors of the Canal Zone during 1949 and 1950. Collections were made throughout the dry and wet seasons of both years. The dry season in the Canal Zone usually extends from December to May and the wet season extends from May to December.

## Collecting Methods

Larval collections of mosquitoes were made each week on each Army post by technicians of the 25th Preventive Medicine Survey Detachment and native larval hunters supervised by these technicians. The larval collections were obtained from various types of breeding places, including streams, ditches,

[1] The authors wish to express their appreciation to Colonel Francis P. Kintz, MC, Surgeon of the United States Army Caribbean for making this work possible and to the technicians of the 25th Preventive Medicine Survey Detachment for valuable assistance.

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ground pools, tree holes, tin cans, tires, leaf axils and many other miscellaneous containers.

Adult mosquitoes were collected in horse-baited traps of the Egyptian type, as described by Bates (1944), New Jersey light traps and by hand on approaching the collector to bite. Horse-baited traps were operated four nights each week throughout the entire period on Army posts on both the Atlantic and Pacific sides of the Isthmus for the purpose of evaluating the mosquito problem and measuring the effectiveness of control measures used against *Anopheles albimanus* Wied., the principal vector of malaria in this region. Light traps and hand collections were employed as supplementary measures. Table 1 contains a list of the species and numbers of adults and larvae collected and identified during 1949 and 1950 as well as the months during which the collections were made.

*Horse-baited trap versus light trap.*—Pritchard and Pratt (1944) found a light trap to be generally superior to an animal-baited trap for collecting *A. albimanus* in Puerto Rice. Table 2 gives the total mosquito catches obtained with a New Jersey light trap and a horse-baited trap operated at Madden Dam, Canal Zone from October, 1948 to October, 1949 for a total of 188 nights of operation. In this table *Anopheles* (*Nyssorhynchus*) spp. includes both *A. albimanus* and *A. triannulatus* Neiva and Pinto; however, the former species was predominant in the horse-baited trap as determined by examinations of eggs obtained from ovipositing females. The females of these two species cannot at this time be separated with certainty except by examination of the eggs.

The light trap was equipped with a 25-cycle electric fan and a 40-watt white frosted lamp. The same horse was used in the animal bait trap throughout the study. Madden Dam was selected for this study since no mosquito control was being done in this area. Since this is not a military installation the catches are not included in the totals in Table 1.

The horse-baited trap proved superior to the light trap for catching both *A. albimanus* and *A. punctimacula* Dyar and Knab in this area of Panama. It is also interesting to note that catches of *Mansonia titillans* (Walker) and *Aedes taeniorhynchus* (Wied.), two important pest mosquitoes of the area, were much greater in the horse-baited trap than in the light trap.

Although there is little published information on the use of the New Jersey light trap in the Canal Zone and adjacent areas, many mosquito control workers in this region have contended that these traps were not satisfactory for sampling populations of *A. albimanus, A. punctimacula* and important pest species. Our findings at Madden Dam seem to provide some justification for this contention. However, the writers have found the light trap to be an invaluable supplementary sampling device in this area because of its ease of operation and the great variety of species taken, many of which are rarely or never taken in animal-baited traps.

## NOTES ON GENERA AND SPECIES

Genus *Chagasia* Cruz.—Represented in this area by a single species, *C. bathanus* Dyar. Larvae are found mostly during the dry season, January to

April, along the margins of swift streams resting parallel to the bank or some object rather than "headon." Adults were not taken in these collections on Army posts but were taken on several occasions by Galindo *et al.*, (1950) biting mostly in the forest canopy during the daytime.

Genus *Anopheles* Meigen.—Represented by 10 species in the adult collections and 11 species in the larval collections. *A. albimanus* Wied. was the most common species encountered as adults on Army posts, occurring throughout the year, but was more numerous during the rainy season when rain pools were common. *Anopheles eiseni* Coquillett was abundant in the larval stage throughout the year, breeding in rot cavities of trees, rock holes, ground pools with leaf covered bottoms and in other similar habitats. The adults were rarely encountered since they are seldom attracted with animal bait. Males and females were rather numerous on the Atlantic side where they could be found resting in tree buttresses during the daytime. *Anopheles kompi* Edwards was frequently taken during the dry season on both sides of the Isthmus breeding in intermittent pools with leaf covered bottoms in hill streams. *Anopheles strodei* Root, *A. oswaldoi* Peryassu and *A. neivai* H. D. and K. were rarely taken on Army posts. The writers have encountered *A. oswaldoi* in large numbers in Mojingo Swamp, a large freshwater marsh on the lower Chagres River near Fort Sherman. The adults of *A. neivai* have been taken in horse-baited traps by the writers on several occasions on the Atlantic side where they breed in wild pineapple (*Ananas magdalenae*).

Genus *Toxorhynchites* Howard.—This genus is represented by a single species in the larval collections, *T. hypoptes* Robineau-Desvoidy. This species is primarily a tree hole breeder and is usually abundant during the rainy season, May to December.

Genus *Trichoprosopon* Theobald.—Adults of *T. espini* (Martini), *T. magnum* (Theobald) and *T. longipes* (Fabricius) were occasionally taken while attacking man in the forest or in horse-baited traps located in or near wooded areas. The breeding habits of these species are rather fully described by Galindo *et al.*, (1951).

Genus *Sabethes* Robineau-Desvoidy.—Represented by a few adult specimens of *S. cyaneus* (Fabricius) and *S. tarsopus* Dyar and Knab taken in horse-baited traps operated near wooded areas. The members of this genus are principally inhabitants of the deep forests (Galindo *et al.*, 1951).

Genus *Wyeomyia* Theobald.—This genus includes a large number of species restricted to the jungle or heavily forested areas where they breed principally in tree holes and the leaf axils of various plants. The adults of several species are attracted to man in these areas and are frequently taken in animal-baited traps situated in or near the jungle. Since they breed in small collections of water the larvae are rarely found except during the rainy season, May to December.

Genus *Limatus* Theobald.—Represented by two species in this area, *L. asulleptus* Theob. and *L. durhamii* Theob. The larvae of both species develop

in tree holes, fruit husks, fallen leaves and similar containers in the forest. Larvae are occasionally encountered during the dry season where water is available for their development but are much more abundant during the rainy season. The adults are occasionally attracted to human collectors in the jungle and are frequently taken in animal-baited traps operated near the jungle.

Genus *Uranotaenia* Lynch Arribalzaga.—Represented in these collections by five species of adults and three species in the larval stage. The adults were all taken with the New Jersey light trap except for a single specimen of *U. geometrica* Lutz captured in a horse-baited trap at Madden Dam. *U. nataliae* Lynch Arribalzaga appears to be rare in the area and was taken only twice during these surveys.

Genus *Orthopodomyia* Theobald.—Represented by a single species in these collections, *O. fascipes* Coquillett, which breeds in tree holes in the forest. Breeding of this species is limited to larger holes where the water persists for long periods during the dry season but is general throughout the rainy season. The adults were found by the writers on many occasions in the Republic of Panama resting in tree buttresses during the daytime but their feeding habits have not been observed.

Genus *Mansonia* Blanchard.—*Mansonia titillans* (Walker) is one of the most important pest mosquitoes found at Army installations in the Canal Zone. The species is present throughout the year but more numerous during the dry season. The larvae have been collected in Panama and elsewhere on many occasions clinging to the roots of *Pistia*. However, since this plant is rather difficult to find in many of the areas where adults are numerous, it must be assumed that heavy breeding is taking place in other plant associations. *Mansonia fasciolatus* (Lynch Arribalzaga) and *M. nigricans* (Coquillett) are more restricted than *M. titillans* in their distribution in this area. All three species are readily attracted to horse-baited traps and light traps. *Mansonia* spp. are extremely difficult to control in the immature stages and control directed against the adults is not always effective.

Genus *Aedomyia Theobald*.—Represented by a single species in the collections, A. *squamipennis* Lynch Arribalzaga. The adults are readily attracted to light traps and are taken on occasions in animal-baited traps. The larvae are common during the dry season where they are found in floating river vegetation, often associated with *A. albimanus* and *Culex erraticus* Dyar and Knab.

Genus *Psorophora* Robineau-Desvoidy.—The members of this genus are rarely abundant in this area and seldom constitute problems requiring the application of control measures.

Genus *Aedes* Meigen.—During this work nine species were taken as adults and six species in the larval stage. *A. taeniorhynchus* is the most important pest species of the group and occurs in large numbers on both sides of the Isthmus following high tides during certain seasons of the year. Adults and larvae may be found any time during the year but a large brood is usually

produced following the onset of the rainy season in May or June and one or more smaller broods may appear during the late summer and fall months. Although this species breeds mostly in marshes affected by the ocean tides, some breeding also occurs in freshwater pools unaffected by the tides.

*Aedes angustivittatus* Dyar and Knab reaches its greatest abundance during the rainy season from May to September, breeding in freshwater pools in low woodland areas. *Aedes leucocelaenus* Dyar and Shannon, *A. leucotaeniatus* Komp, *A. terrens* (Walker) and *A. septemstriatus* Dyar and Knab breed mostly in rot cavities of trees and the adults are rarely found outside wooded areas. *Aedes fluviatilis* (Lutz) breeds in rock holes along rivers.

Genus *Haemagogus* Williston.—Four species of this genus are represented in our collections (Table 1). *Haemogogus equinus* Theobald, *H. argyromeris* Dyar and Ludlow and *H. lucifer* H. D. and K. are common in timbered areas on Army posts during the rainy season. Although these species are largely restricted in their breeding to rot cavities in trees, *H. argyromeris* also breeds in small collections of water in buckets, tubs, cans and other similar containers. *H. argyromeris* was particularly abundant during 1949 and 1950 on Flamenco Island near Fort Amador (Galindo *et al.*, 1951).

*Haemagogus chalcospilans* Dyar is apparently restricted in its breeding to small collections of water in rot cavities in mangrove trees in or near tidal marshes. All four species of *Haemagogus* listed in Table 1 readily attack man in wooded areas near their breeding places. The females of *H. chalcospilans* have the peculiar habit of attacking man only in the region of the head and shoulders.

Genus *Culex* Linnaeus.—Larval collections of *Culex* are given in Table 1. No attempt was made to separate the adults of the different species when taken in light or animal-baited traps. *Culex coronator* Dyar and Knab, *C. elevator* Dyar and Knab, *C. corniger* Theobald, *C. nigripalpus* Theobald and *C. cinquefasciatus* Say were the more common species of *Culex* encountered on Army posts in the larval stage. With the exception of *C. quinquefasciatus,* none of these speceis appear to have much importance as pests in the area.

Genus *Deinocerites* Theobald.—Adult specimens of *D. cancer* Theobald and *D. pseudes* Dyar and Knab were occasionally taken in horse-baited traps. Both species breed in saltwater in crab holes in the tidal marshes.

## SUMMARY

Adult mosquitoes collected by hand and with the aid of horse-baited and light traps and larval collections made each week on Army posts in the Canal Zone are given with months of occurrence for each species.

A comparison is made of mosquito catches obtained with horse-baited and light traps operated at Madden Dam, Canal Zone, over a period of one year.

Distribution, seasonal abundance and biology are discussed for the important species of the different genera represented in the mosquito collections made by Army personnel in the Canal Zone during 1949 and 1950.

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TABLE 1.—Mosquito collections at Army installations in the Canal Zone during 1949 and 1950

| Species | Adults: Months of Collection | Adults: Total | Larvae: Months of Collection | Larvae: Total |
|---|---|---|---|---|
| Chagasia bathanus | | | Jan.-Apr., June, Sept., Nov. | 24 |
| Anopheles kompi | | | Jan.-Mar., Sept. | 52 |
| Anopheles eiseni | July | 1 | Jan.-Dec. | 3,187 |
| Anopheles pseudopunctipennis | Jan., Feb., May, June, Aug., Dec. | 51 | Mar.-May, July | 71 |
| Anopheles apicimacula | Jan.-Dec. | 1,254 | Jan.-Dec. | 2,622 |
| Anopheles punctimacula | Jan.-Dec. | 1,270 | Jan.-Dec. | 1,193 |
| Anopheles neomaculipalpus | Jan., July, Sept., Nov., Dec. | 34 | Jan.-Dec. | 351 |
| Anopheles argyritarsis | Jan.-Aug., Nov., Dec. | 88 | Jan.-Dec. | 353 |
| Anopheles albimanus | Jan.-Dec. | 2,515 | Jan., Mar., May-Aug., Oct.-Dec. | 280 |
| Anopheles aquasalis | Mar.-Dec. | 1,201 | Apr.-June, Aug.-Nov. | 85 |
| Anopheles oswaldoi | | | Jan., Sept., Dec. | 11 |
| Anopheles triannulatus | Jan., Feb., May | 4 | | |
| Anopheles strodei | | | Jan., Feb., Dec. | 44 |
| Anopheles neivai | Aug., Sept., Dec. | 8 | | |
| Toxorhynchites hypoptes | | | Jan., Feb., Apr.-Dec. | 190 |
| Trichoprosopon longipes | Nov. | 1 | | |
| Trichoprosopon magnum | Nov. | 1 | | |
| Trichoprosopon espini | Sept., Oct., Dec. | 27 | | |
| Trichoprosopon spp. | Apr., May, July-Oct. | 28 | Jan., Feb., May-Dec. | 796 |
| Sabethes cyaneus | Aug. | 3 | | |
| Sabethes tarsopus | Aug. | 2 | | |
| Wyeomyia arthrostigma | June-Sept. | 29 | | |
| Wyeomyia hemisognasta | Aug. | 1 | | |
| Wyeomyia (Wyeomyia) spp. | June, Aug., Sept., Dec. | 13 | | |
| Wyeomia personata | May, Aug. | 9 | Dec. | 5 |
| Wyeomia (Dendromyia) spp. | Sept., Nov., Dec. | 5 | | |

Table 1.—(*Continued*)

| Species | Adults: Months of Collection | Adults: Total | Larvae: Months of Collection | Larvae: Total |
|---|---|---|---|---|
| Wyeomia spp. | | | Feb., Apr., Dec. | 69 |
| Limatus asulleptus | Aug., Dec. | 2 | May, June | 46 |
| Limatus durhamii | June-Oct. | 15 | Jan.-Dec. | 1,112 |
| Uranotaenia coatzacoalcos | Feb., Mar., June | 3 | Mar., June-Oct., Dec. | 77 |
| Uranotaenia geometrica | Jan., May-Aug., Oct. | 23 | Jan.-May, Aug.-Dec. | 183 |
| Uranotaenia lowii | Jan.-May, July-Oct. | 24 | | |
| Uranotaenia nataliae | Feb., May | 2 | | |
| Uranotaenia pulcherrima | Feb., Mar., May, June | 20 | July, Aug., Nov. | 13 |
| Orthopodomyia fascipes | | | Jan., Mar., May-Sept., Nov., Dec. | 68 |
| Mansonia titillans | Jan.-Dec. | 68,458 | Jan. | 62 |
| Mansonia fasciolata | Jan., Feb., Apr.-Dec | 801 | | |
| Mansonia nigricans | Jan.-Oct. | 94 | | |
| Aedomyia squamipennis | Feb.-Oct. | 121 | Jan., Feb. | 33 |
| Psorophora cilipes | Aug. | 1 | | |
| Psorophora lineata | Sept. | 1 | | |
| Psorophora ferox | Mar., May-Aug., Oct. | 32 | May-Nov. | 79 |
| Psorophora lutzii | May-Sept., Nov. | 27 | June, July | 9 |
| Psorophora cingulata | Jan., June-Dec. | 80 | | |
| Aedes leucocelaenus | Aug., Oct.-Dec. | 4 | | |
| Aedes leucotaeniatus | July | 1 | | |
| Aedes terrens | Apr., May, Aug., Sept., Nov. | 17 | Jan., Apr., Dec. | 791 |
| Aedes fluviatilis | July, Sept. | 2 | | |
| Aedes fulvus | July-Sept., Dec. | 34 | | |
| Aedes serratus | May-Dec. | 49 | Aug., Sept., Nov., Dec. | 30 |
| Aedes angustivittatus | Jan., Mar.-Dec. | 1,039 | Dec. | 1 |
| Aedes euplocamus | May | 1 | Sept. | 9 |

Table 1.—(*Continued*)

| Species | Adults Months of Collection | Total | Larvae Months of Collection | Total |
|---|---|---|---|---|
| Aedes taeniorhynchus | Jan.-Dec. | 22,381 | Mar.-Dec. | 1,556 |
| Aedes septemstriatus | | | Dec. | 15 |
| Haemagogus equinus | May-Sept., Nov., Dec. | 50 | Apr.-Dec. | 86 |
| Haemagogus argyromeris | June, Nov. | 5 | Jan., Feb., May-Dec. | 193 |
| Haemagogus chalcospilans | Aug. | 1 | | |
| Haemagogus lucifer | Mar., May-Dec. | 97 | Jan., Mar., May-Dec. | 160 |
| Culex allostigma | | | Feb.-Dec. | 97 |
| Culex corniger | | | Jan.-Dec. | 1,946 |
| Culex coronator | | | Jan.-Dec. | 21,715 |
| Culex declarator | | | Jan.-Dec. | 676 |
| Culex interrogator | | | Feb.-July, Sept.-Nov. | 125 |
| Culex mollis | | | Jan.-Dec. | 610 |
| Culex nigripalpus | | | Jan.-Dec. | 1,614 |
| Culex quinquefasciatus | | | Jan.-Dec. | 1,280 |
| Culex erraticus | | | Jan., Feb. | 103 |
| Culex elevator | | | Jan.-Dec. | 2,287 |
| Culex corrigani | | | July-Dec. | 24 |
| Culex pilosus | | | May-July, Nov., Dec. | 78 |
| Culex secundus | | | May, June, Sept.-Dec. | 186 |
| Culex vexillifer | | | Oct., Nov. | 5 |
| Culex (Melanoconion) spp. | | | Feb., Apr.-Nov. | 754 |
| Culex spp. | | | Jan.-Dec. | 28,809 |
| Deinocerites cancer | Aug. | 5 | May-Aug., Oct., Dec. | 85 |
| Deinocerites pseudes | Apr.-Aug. | 267 | June, Aug. | 11 |
| | Total | 100,202 | Total | 74,261 |

TABLE 2.—Comparison of adult mosquito catches with a New Jersey light trap and a horse-baited trap at Madden Dam, Canal Zone, October 1948 to October 1949

| Species[1] | Light Trap Male | Light Trap Female | Hore-baited Trap Female |
|---|---|---|---|
| Anopheles eiseni | | 2 | |
| Anopheles pseudopunctipennis | | 1 | |
| Anopheles apicimacula | 1 | 9 | 92 |
| Anopheles punctimacula | | 7 | 431 |
| Anopheles neomaculipalpus | | 4 | 61 |
| Anopheles argyritarsis | | | 5 |
| Anopheles (Nyssorhynchus) spp. | 2 | 24 | 998 |
| Toxorhynchites superbus | | | 1 |
| Trichoprosopon digitatum | | | 1 |
| Limatus durhamii | | 3 | 2 |
| Uranotaenia coatzacoalcos | | 1 | |
| Uranotaenia geometrica | | 6 | 1 |
| Uranotaenia lowii | 1 | 16 | |
| Uranotaenia pulcherrima | 1 | 19 | |
| Mansonia titillans | 10 | 2,888 | 59,628 |
| Mansonia fasciolata | | 27 | 10 |
| Mansonia nigricans | 1 | 41 | 34 |
| Aedomyia squamipennis | 6 | 98 | |
| Psorophora lineata | | | 1 |
| Psorophora ferox | | 1 | 5 |
| Psorophora lutzii | | | 24 |
| Psorophora cingulata | | | 1 |
| Aedes terrens | 1 | | |
| Aedes fluviatilis | | | 3 |
| Aedes serratus | | 2 | 1 |
| Aedes angustivittatus | 1 | 63 | 1,201 |
| Aedes taeniorhynchus | 14 | 141 | 2,812 |
| Haemagogus lucifer | | | 11 |
| Total | 38 | 3,353 | 65,323 |

[1] Unidentified *Culex* are not included.

# Descriptions of New Species and Notes on North American Orthoptera

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## Phasmidae

Through the courtesy of Mr. A. D. Barnes, Director of Dade County Parks, I have been permitted to do restricted collecting of insects in Matheson Hammock, a jungle about five miles south of the university. On night excursions I have observed the large walkingstick insect, *Aplopus mayeri* Caudell, in both immature and mature stages. Some were observed feeding on the leaves of black ironwood (*Krugiodendron ferreum*). A female taken *in coitu* measures 160 mm. in length. Caudell described *A. mayeri* from specimens taken on Dry Tortugas and it has been reported from several localities on the keys and from Everglades in Collier County. Hitherto this phasmid has been considered as restricted in its feeding to bay cedar (*Suriana maritima*). Very recently I captured an adult male on buttonwood (*Conocarpus erecta*) growing along a road through a mangrove swamp. No *Suriana* or *Krugiodendron* is to be found within several miles of this spot.

## Gryllidae

Soon after moving into a newly-built house in September 1948 I noticed tiny crickets were present. The first of these taken and examined proved to be *Cycloptilum squamosum zebra* Rehn and Hebard, and I assumed without study that several specimens subsequently captured were of the same species. Recently, however, on tracing a feeble song I found the singer to be a cricket evidently different from *zebra*. Examination of it and the small series already collected showed that three males and five females of *Cycloptiloides americanus* had been taken.

*C. americanus* was described by Saussure as from Cuba, and Rehn and Hebard in 1912 listed additional records, including Vera Cruz, Mexico and San José del Cabo, Lower California, but Hebard did not treat the species in his 1931 synopsis of the Mogoplistini of the United States. The present report is apparently the first record of its occurrence in this country. All the houses in our vicinity were built in 1948 and it thus appears probable that *C. americanus* was already present in the pine woods which was removed prior to building. The records of capture extend from March 1949 to October 1950 and the presence of immature individuals is evidence of reproduction. Evidently the little insect is established and should prosper on the crumbs of animal crackers scattered by my small daughters.

## TETTIGONIIDAE

### **Microcentrum minus** sp. n.

Figs. 1, 2

*Holotype:* Male, Hidalgo County, Texas IV-7-50 (D. J. & J. N. Knull).

Similar to *M. rhombifolium* (Saussure) but much smaller and differing particularly in the cerci and subgenital plate. Head with fastigium of vertex flat, narrowed anteriorly and at apex little wider than the first joint of antenna. Front margin of pronotum weakly bisinuate, roundly advanced at middle; lateral lobes perpendicular, deeper than long. Tegmen with the median vein terminating in sutural margin, its stridulatory area similar to that of *rhombifolium* but with the veins less strongly developed. Supra-anal plate triangular, vertical, with a deep median groove in basal two-thirds, its tip acutely rounded and reflexed. Cercus broad at base, tapering rapidly in basal third to the almost straight shaft, the apex of the shaft abruptly incurved with rounded tip, which bears a triquetrous tooth. The shaft of the cercus is flattened, hence appears much narrower in lateral than in dorsal view. Subgenital plate narrow, with a strong carina and deeply v-excised apex; styles short. Front femur with three small, widely-spaced spines on distal third of ventrocephalic carina, its ventrocaudal carina unarmed. Middle femur similarly armed. Caudal femur with six small, widely-spaced spines on distal half of each ventral carina (five on ventrocephalic of left femur). The insect was undoubtedly uniform green in life but now shows diffuse brown areas due to postmortem changes.

*Measurements* (mm.): Length of body 20, of pronotum 5.5, of tegmen 34.2, of hind femur 18.3; maximum width of tegmen 10.3.

*Allotype:* Female, data as for type.

This specimen differs from the holotype only in its greater body length, broader tegmina, without stridulatory area, and terminal abdominal structures. The ovipositor is very similar to that of *M. suave* as described and figured by Hebard (1923, p. 336; p. 329, fig. 9).

*Measurements* (mm.): Length of body 25.4, of pronotum 5.7, of tegmen 35.5, of hind femur 19.6; maximum width of tegmen 11.

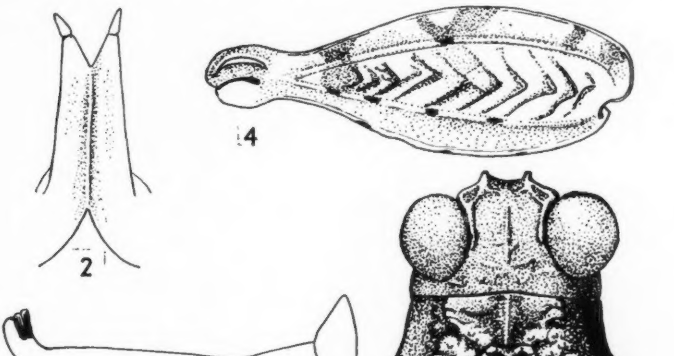
This species is probably most closely related to *M. suave* Hebard from which it differs in its broader tegmina, shorter hind femora and, in the male, straight cercal shaft and carinate and acutely excised subgenital plate.

## LOCUSTIDAE

### XANTHIPPUS CORALLIPES (Haldeman)

Numerous names have been applied to specimens of this species, originally described from Utah material. Many of these names have been relegated to synonymy but persisting in racial status are *pantherinus, latefasciatus, leprosus, cupidus* and *altivolus*. Rather than showing geographic correlations these "races" occur in certain environments over much of the range of the species. *X. corallipes buckelli* Hebard (1928, p. 241), however, is a definite geographic race of the extreme northwestern part of the range of the species.

Two seasons of collecting in the vicinity of Las Vegas, New Mexico yielded interesting lots of *corallipes*. At Montezuma, in the Gallinas Canyon, I took small, dark specimens, the males about an inch in overall length, the females about one and one-eighth inches but with tegmina not shorter than the body. According to the descriptions these specimens are referable to *cupidus* or *altivolus*. Not over eight miles from Montezuma, on the plains northeast of Las Vegas, are found individuals best referred to the race *leprosus*, while at La Liendre, twenty miles southeast of Las Vegas, occur individuals of similar size but lighter coloration and among these some specimens showing the elytral pattern and dark inner face of the hind femur characteristic of the race *pantherinus*. While the three localities cited are close together they undoubtedly have different moisture characteristics; the plains vegetation is wholly grass, including grama, while at La Liendre grass is scarce and yucca abundant. Quite certainly the floor of Gallinas Canyon, in addition to greater moisture, has lower average temperatures. Subject to air drainage from high mountains and protected from direct sunlight for much of the day




Figs. 1-4.—1. *Microcentrum minus* sp. n.. a. Right cercus of holotype, dorsal view. b. Detail of apical tooth of cercus; 2. *M. minus* sp. n. Subgenital plate of holotype, ventral view; 3. *Agymnastus haemopterus* sp. n. Head and pronotum of holotype, dorsal view; 4. *A. haemopterus* sp. n. Right caudal femur of holotype.

by the canyon's steep walls, the water of Gallinas Creek remains frozen long after ice has disappeared elsewhere.

It appears from examination of these and other specimens from New Mexico, Arizona, Utah and Nevada that about all gradations of size, elytral maculation and wing length may be encountered within rather small areas widely scattered in the range of the species. While genetic bases for these differences are not ruled out, it seems more probable, in the light of such experiments as Faure's, that *X. corallipes* is a species of great adaptability and plasticity and the races mentioned above are ecophenes rather than genetic units.

In spite of the above discussion there remains, in my opinion, a form of *corallipes* which, like *buckelli* Hebard, shows distinctive characters correlated with geographic distribution. It has been reported by Rehn and Hebard (1909, p. 438) as *Hippiscus pardalinus* (Saussure).

### **Xanthippus corallipes miniatus** subsp. n.

*Holotype:* Male, June Lake, California, VI-20-48 (G. P. McKenzie).

Slenderer than is usual in the species. Head much less rugose than in other races, the vertex and occiput practically smooth except for a feeble median carina, which is extended anteriorly through the fastigium of the vertex. Fastigium as long as broad, its walls well elevated, its disc smooth except for the median carina. Frontal costa shallowly sulcate, expanded between the antennal bases and abruptly constricted a short distance below the ocellus. Front and clypeus smooth, sparsely punctured. Pronotum with median carina low, almost obliterated between the sulci, very low on posterior part of metazone. Hind margin of pronotum right angled. The disc of the metazone is granulately rugose without the strong verrucae usual in the species. The most notable feature of coloration is the vermilion wing disc, beyond which is a very narrow black band interrupted along several of the veins and ending considerably short of the anal angle. The humeral taenia of the wing is extended not quite halfway to the base of the wing. At its apex the wing bears a rounded dark blotch and just proximad to this two small, dark spots transversely arranged. Tegmen with four dark crossbars in proximal half; these almost reach the sutural margin but are broadly interrupted by the pale anal stripe. The distal half of the tegmen bears four clearly delimited dark crossbars, which end posteriorly at the anal stripe. Posterior femur with three groups of dark spots on outer face, the middle and distal of which are continuous with dark bars on the upper flange. Lower and inner face of femur and lower internal genicular lobe carmine red. Hind tibia largely yellow with a few red spots internally near base. The bases of the spines of the internal series are pink; these pink areas are continued as a streak which broadens to cover the distal fourth of the inner and upper face of the tibia.

*Measurements* (mm.): Length of body 29, of pronotum 6.1, of hind femur 14.

*Allotype:* Female, data as for holotype.

Differs from holotype in the usual sexual features: terminal abdominal

appendages, larger size, more robust form and shorter antennae. Vertex of head slightly uneven. Disc of metazone of pronotum with a few low verrucae, its posterior margin slightly obtuse. Color similar to that of holotype but with the inner face of caudal tibia more extensively pink.

*Measurements* (mm.): Length of body 41.4, of pronotum 8.8, of hind femur 18.3.

Five males collected at June Lake and Mono Lake and three females collected at June Lake by Mr. McKenzie are designated paratypes. The paratypic series offers no features deserving further comment.

It is surprising that the large insect described below has escaped the attention of entomologists. Probably its maximum abundance is in early spring before orthopterists take to the field. In appearance this insect is somewhat like a *Xanthippus* but it has certain morphological features most similar to those of *Agymnastus ingens* (Scudder).

### **Agymnastus haemopterus** sp. n.

*Holotype:* Male, Hesperia, Calif., IV-14-48 (G. P. McKenzie).

Head small, not at all elevated above the pronotum, eyes moderate in size, prominent, antennae about as long as head and pronotum combined, heavy and not at all attenuate. Frontal costa fairly deeply sulcate with flaring carinae, which are abruptly but not greatly constricted below the ocellus, thence gently divergent to the clypeal suture. Above, the frontal carinae are continuous with the bounding ridges of the foveolae, which are distinctly impressed. Between the foveolae the frontal costa is divided by an elongate tubercle and separated from the vertical fastigium by low, transverse ridges. Fastigium with a fine median carina and high walls, which extend posteriorly to mid-length of the eyes. Occiput rough. Pronotum over two and a half times as long as head, its hind margin acutely rounded and a little reflexed, its median carina strong. On the metazone the lateral carinae are elevated and callous, the hind margin much thickened and continuous at apex with the subcristate median carina, disc with low, rounded tubercles. The median carina is visible on the posterior lobe of the prozone, which is here deeply scutellate. On the anterior lobe of the prozone the carina is cristate. The disc of the prozone is occupied by heavy callosities. Tegmina and wing narrower than in *Xanthippus*. Hind femur short, stout, broadly flanged above and below, its outer face very rough. In color the insect is generally griseous, some of the pronotal callosities yellowish and with patches of similar color on the head. Hind femora buffy on outer face with a complete black band before the apex, a broad, less defined black area at middle and two smaller, dark patches on the upper flange near base; lower and inner faces deep black with preapical paler band which is red internally and yellow below. Hind tibiae bright red with black-tipped spines. Tegmen brownish gray, subhyaline in distal half of sutural region. The costal field has a short, pale bar at the humeral angle, a broader, pale bar just beyond the angle, while the distal half of the tegmen has an elongate pale area along the discoidal vein. Wing narrow, orange-red on the disc, with a narrow, fuscous band which fails to reach the anal angle. The humeral tenia is broad and reaches three-fourths of

the distance to the base of the wing. Apical fourth of wing hyaline with dark veins, its extreme apex smoky.

*Measurements* (mm.): Length of body 21, of pronotum 6, of hind femur 10, of tegmen 25.5; breadth of hind femur 4.1, of metasternum 6.1.

*Allotype:* Female, no data (A. T. McClay).

Much larger than the holotype male and differing from it chiefly in quantitative manner. Head, across the eyes, little more than half as broad as greatest breadth of pronotum, in length about one-third that of pronotum. Frontal costa broad, feebly sulcate. Fastigium of vertex with high walls and a pair of transverse ridges between the eyes. Occiput tuberculate and verrucose, numerous ridges radiating from the hind margins of the eyes. Pronotum rapidly expanding to base of tegmina, its posterior margin slightly acute, its lateral carinae strong but not as elevated and calloused as in the male, its median carina evident throughout but intersected twice. Hind femur massive, its flanges, especially the lower, strongly expanded, its outer face coarsely ridged. Coloration similar to that of the type except that the pale areas of the tegmina are extended as spots behind the discoidal vein and there is an almost complete pale crossbar just beyond mid-length. The red of the wing disc is also deeper than in the holotype.

*Measurements* (mm.): Length of body 53, of pronotum 14, of tegmen 43, of hind femur 24; breadth of hind femur 6.3, of metasternum 15.

A male specimen collected in Mint Canyon, Los Angeles County, VI-22-49 by H. E. Cott is designated a paratype. Its coloration is more intensive than that of the holotype and the pale areas of the distal half of the tegmen consist of three small spots behind the discoidal vein. The hind margin of the pronotum is right angled, the tubercles of the metazonal disc are stronger and the hind femur broader than in the holotype.

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# A New Albinistic Crayfish of the Genus Cambarus from Southern Missouri with a Key to the Albinistic Species of the Genus (Decapoda, Astacidae)[1]

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Of the previously known albinistic species of the genus *Cambarus* (*C. ayersii, C. setosus, C. hamulatus, C. cryptodytes*, and *C. cahni*) two are inhabitants of the Missouri Ozarks, and have been reported from several caves in the southwestern part of the state. While considerable confusion as to the status of *C. ayersii* and *C. setosus* still obtains, it is clear that the new species described below, although having affinities with them, is markedly distinct.

The specimens on which this description is based were collected by Mr. Leslie Hubricht on July 4, 1941, and have been in my collection since early in 1942. Several efforts to obtain additional specimens have failed.

## Cambarus hubrichti[2] sp. nov.

*Cambarus* sp. Hubricht 1950, Bull. Nat. Speleological Soc. (12):17.

*Diagnosis.*—Eyes reduced; albinistic; rostrum without lateral spines, sometimes with small corneous tubercles; sides of carapace with one to several spines on each side; areola about six times as long as broad and about 41% of entire length of carapace with five punctations across narrowest part; antennal scale broad with distal margin of lamellar portion rounded—not straight as in *ayersii* and *setosus;* chelae without conspicuously long setae. See figures 6, 8, and 3 for structure of first pleopod and annulus ventralis.

*Holotypic male, form II.*—Body subovate, somewhat depressed. Abdomen narrower than thorax (18.5-15.2 mm. in widest parts respectively). Width of carapace greater than depth in region of caudodorsal margin of cervical groove (18.1-13.1 mm.). Greatest width of carapace just caudad of caudodorsal margin of cervical groove.

Areola moderately broad (6.4 times longer than wide) with five punctations across narrowest part; cephalic section of carapace about 2.4 times as long as areola; length of areola about 41.9% of entire length of carapace.

Rostrum with slightly convergent margins which are somewhat thickened; lateral spines or tubercles lacking; upper surface concave with scattered setiferous punctations. Acumen sharply set off from rest of rostrum, long, reaching middle of distal joint of peduncle of antennule, and with upturned corneous tip. Subrostral ridges moderately well developed but evident in dorsal aspect for only a short distance at their bases.

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[1] Contribution from the Miller School of Biology, University of Virginia.

[2] It is with pleasure that I name this species in honor of its discoverer, Mr. Leslie Hubricht.

Postorbital ridges short and not prominent, grooved dorsolaterad, and produced cephalad in small acute corneous tubercles. Suborbital angle lacking. Branchiostegal spine small and acute. Lateral surface of carapace with a strong dextral spine and two strong sinistral ones. Surface of carapace punctate dorsad and granulotuberculate laterad; lateral areas of cephalic portion of carapace studded with small tubercles.

Abdomen and carapace subequal in length.

Cephalic section of telson with one spine in each caudolateral corner.

Epistomes subovate with elevated (ventrally) central area; a faint cephalomedian projection present.

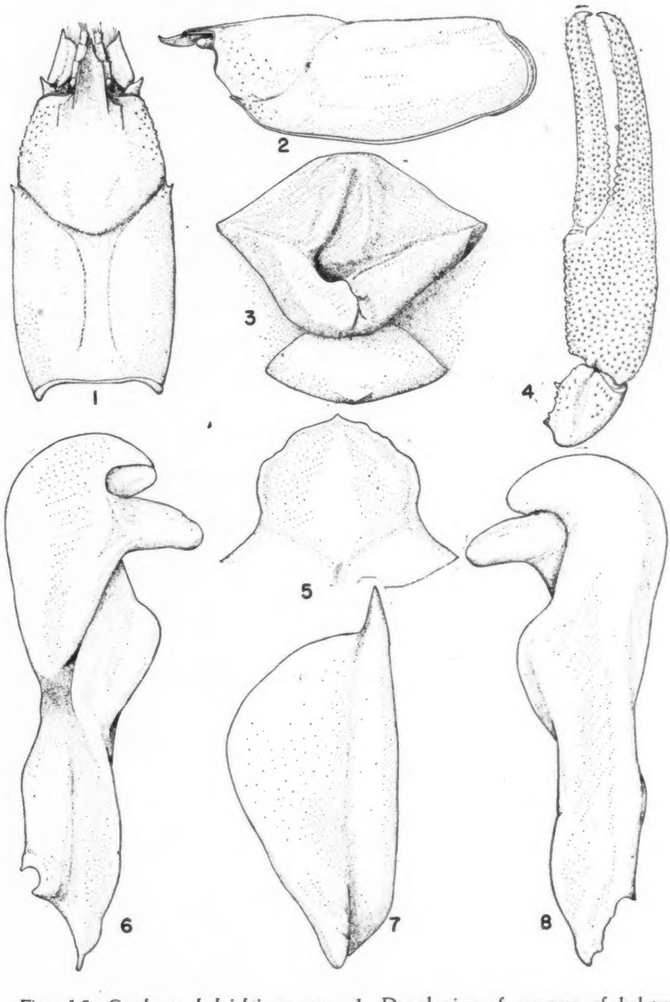
Antennules of the usual form with a small spine on ventral surface of basal segment.

Antennae extend caudad to caudal margin of telson. Antennal scale (fig. 7) of moderate length and breadth, and with a strong spine on outer distal margin; mesial margin of lamellar portion evenly rounded.

Chela elongate, subovate in cross section with palm slightly inflated; mesial and lateral margins of propus with tubercles; mesial half of upper and lower surfaces of propus with setiferous tubercles, and lateral portion with setiferous punctations. Acute tubercle present on lower surface of palm at base of dactyl. Inner margin of palm with a row of 15 tubercles which are slightly larger than those of the rows lying above and below it. Fingers not gaping. Upper surface of immovable finger with a submedian longitudinal ridge bearing a row of small setiferous punctations, and flanked on both sides by scattered somewhat larger ones. Lateral margin of immovable finger also bearing a longitudinal ridge flanked similarly as the ridge on the upper surface. Lower surface of immovable finger V-shaped in cross section without a well-defined ridge but bearing numerous setiferous punctations. Opposable margin of immovable finger with a single row of 25 tubercles, and in addition a somewhat larger one lying below this row slightly proximad of midlength; lying between and below the tubercles of the just-mentioned row are crowded minute denticles. Upper and lower surfaces of dactyl similar to the corresponding surfaces of the immovable finger; however, mesial margin tuberculate proximad and punctate distad with no ridge evident. Opposable margin of dactyl with a row of 30 tubercles between and below which are minute denticles. For the most part the tubercles are progressively smaller distad.

Carpus longer than broad with a prominent longitudinal furrow above; entire surface of podomere with widely scattered setiferous punctations. Mesial upper surface with an irregular group of low tubercles; mesial surface with a somewhat larger proximal tubercle and a trio of them slightly distad of midlength, the largest of the three acute; lower mesial margin with a row of four tubercles, the most distal of which is corneous and acute.

Merus with scattered setiferous punctations on all surfaces. Upper surface with narrow band of scattered tubercles of which two near the distal end are somewhat larger than the others, and on the sinistral merus subacute; lower surface with a mesial row of 17 or 18 tubercles and a lateral one of 10 or 15, with additional tubercles lying between and laterad of the two afore-mentioned rows.



Figs. 1-8. *Cambarus hubrichti* sp. nov.—1. Dorsal view of carapace of holotype; 2. Lateral view of carapace of holotype; 3. Annulus ventralis of allotype; 4. Upper surface of distal portion of cheliped of holotype; 5. Epistome of holotype; 6. Mesial view of first pleopod of holotype; 7. Antennal scale of holotype; 8. Lateral view of first pleopod of holotype.

Ischiopodite of first pereiopod with an upper row of five tubercles and a lower one of five or eight.

Hooks on ischiopodites of third pereiopods only; hooks strong and simple.

Coxa of fourth pereiopod with a well-developed caudomesial prominence.

First pleopod extends cephalad to coxopodite of third pereiopods when abdomen is flexed. Tip terminating in two distinct parts which are bent at right angles to the main shaft of the appendages (figs. 6 and 8). Mesial process somewhat inflated and extends distinctly caudad of the tip of the central projection. Neither element corneous.

*Allotypic female.*—Differs from the holotype in the following respects: Epistome while subovate more emarginate. Inner margin of palm of chela with a row of 14 tubercles. Opposable margin of immovable finger with a single row of 23 or 25 tubercles with two or three larger ones lying below this row. Opposable margin of dactyl with a row of 25 tubercles. Mesial surface of one carpus as in holotype and on other a group of eight small tubercles with an additional acute one. Mesial row of tubercles on lower surface of merus consists of 18 and the lateral one of 11 or 18. Ischiopodite with a row of five or eight tubercles.

Annulus ventralis with a well-developed caudal ridge and smaller longitudinal ones on each side of median line. Sinus originates considerably caudad of cephalic margin at caudal end of the dextral longitudinal ridge, curves dextrad to make a sharp turn to the median line where it forms an arc across the caudal ridge, and reaches the caudal margin of the annulus just sinistrad of the median line (fig. 3).

Measurements.—As follows (in millimeters):

| | Holotype | Allotype | ♂ Paratype | ♀ Paratype |
|---|---|---|---|---|
| Carapace—height | 13.1 | 13.7 | 14.8 | 14.1 |
| width | 18.1 | 18.2 | 18.3 | 18.1 |
| length | 38.2 | 39.1 | 39.5 | 37.2* |
| Areola—length | 16.1 | 16.4 | 16.7 | 16.3 |
| width | 2.5 | 2.6 | 2.7 | 1.8 |
| Rostrum—length | 7.6 | 8.4 | 8.4 | 6.5* |
| width | 3.9 | 4.4 | 4.1 | 4.1 |
| Abdomen—length | 38.2 | 39.9 | 40.5 | 39.0 |
| Right chela— | | | | |
| length of inner margin of palm | 13.6 | 12.9 | 12.1 | 10.8 |
| width of palm | 10.8 | 10.8 | 9.5 | 8.3 |
| length of outer margin of hand | 44.0 | 38.5 | 39.0 | 33.9 |
| length of dactyl | 27.8 | 23.4 | 25.1 | 21.5 |

* Rostrum probably injured.

*Type locality.*—Stream in Lewis Cave, 15 miles northwest of Doniphan, Ripley County, Missouri.

*Disposition of types.*—The holotypic male, form II, and the allotypic female (U.S.N.M. nos. 92295-96) are deposited in the United States National Museum. The two paratypes, one male, form II, and one female, are in my personal collection at the University of Virginia (HHH no. 7-441-3).

*Range.*—This species is known only from the type locality.

*Variations.*—The number of lateral spines on each side of the carapace varies from one to three. In one specimen the acumen is decidedly shorter than those of the other three, and is not upturned—possibly a result of an injury. Although lateral spines are absent on the rostra of all four specimens there are minute corneous tubercles at the base of the acumen in two of them. Greatest width of carapace in the allotype and paratypes near midlength of thoracic portion instead of in region of caudodorsal margin of cervical groove. The epistomes of two of the specimens have no cephalomedian projections. The mesial surfaces of the carpi of the first pereiopods of both the paratypes bear a row of three or four spiniform tubercles instead of the single large one flanked by smaller ones. Cephalolateral surfaces of carapace of both paratypes with spiniform tubercles, in this respect resembling some of the species of the Limosus Section of the genus *Orconectes.*

*Relationships.*—*Cambarus hubrichti* probably has its closest affinities with *Cambarus ayersii* and *Cambarus setosus;* however, it may be readily distinguished from them by possessing a broader areola, a longer rostrum, the weakly-developed setae of the pereiopods, and the markedly-different antennal scale.

KEY TO THE ALBINISTIC SPECIES OF THE GENUS CAMBARUS

1 Rostrum with a median carina ..................................*C. cahni* Rhoades (1941:146)
Range—northern Alabama
1' Rostrum without a median carina ........................................................ 2
2(1') Lateral spines present on rostrum ........................................................ 3
2' No lateral spines present on rostrum ........................................................ 4
3(2) Areola linear; chela conspicuously setose ....................*C. ayersii* Steele (1902:18)
Range—southwestern Missouri
3' Areola broad with four or five punctations in narrowest part; chela not conspicuously setose ...........................*C. hamulatus* (Cope and Packard 1881:880)
Range—southeastern Tennessee and northern Alabama
4(2') Postorbital ridges with spines ..........................................*C. hubricht* sp. nov.
Range—southern Missouri
4' Postorbital ridges without spines ........................................................ 5
5(4') Chela with long, conspicuous setae; lateral spine present on carapace ................. ..............................................*C. setosus* Faxon (1889:237)
Range—southwestern Missouri
5' Setae on chela not conspicuous; small tubercle on each side of carapace .......... ..............................................*C. cryptodytes* Hobbs (1941:110)
Range—northern Florida

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# Zoogeographic Regions of Indiana

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In order to understand the distribution and abundance of game species in Indiana, it is necessary to recognize and delineate the various land regions. The geological development of land formations and the resultant distribution of soil and water have greatly determined the vegetation and present cultural practices. Natural features, combined with activities of man, in turn, exert a profound influence upon the present animal life existing in any given area. Add to this the influence of climate and it is possible to roughly create eleven zoogeographic regions in Indiana.

This state contains 36,045 square miles of land area, besides 280 square miles of rivers and small lakes, and 230 square miles of Lake Michigan. It holds 37th place in size and 12th place in population. It ranks third among the states in proportion of improved land, being surpassed by only Iowa and Illinois.

Malott (1922) describes Indiana as being located towards the eastern edge of the great interior plains of the United States, which stretch between the Rocky Mountains and the Appalachian Highlands. With the exception of about 6,000 square miles in the south-central section, the rest of the state has been glaciated and is relatively smooth, except for some small moranic areas. The glacial till plain covers a large area to the north, but a considerable part of southern Indiana lies on a well-dissected, low plateau. Altitudes range from 313 feet at the mouth of the Wabash River to 1,285 feet in western Randolph County near the Ohio line. About one-tenth of the present drainage goes into the St. Lawrence system and the rest into the Ohio-Mississippi River system.

The climate in Indiana is not subject to as great variations as occur in states with decided differences in elevation. On the average, the temperature is some 15 to 20 degrees higher at the warmest time of the 24-hour day than it is at the coolest (Visher, 1944). The average annual temperature is 52.7° F., with variations from 54.8° F. in southern, to 52.2° F. in central, and 50.1° F. in northern Indiana. During the two coldest months, January and February, northern Indiana averages 7.1° F. cooler than southern Indiana. The state mean temperature for January is 29° F. Minima of zero are experienced fully three times as often near the northern border as along the Ohio River, and minima of –10° F. are six times more frequent. Although all parts of the state have experienced temperatures of –20° F., such cold snaps are rare and of short duration. The date of the average first killing frost is October 5 in northern, and October 15 in southern Indiana. The dates of the average last killing frosts are May 8 and April 21, respectively, in these two sections. The length of the growing season averages about 170 days.

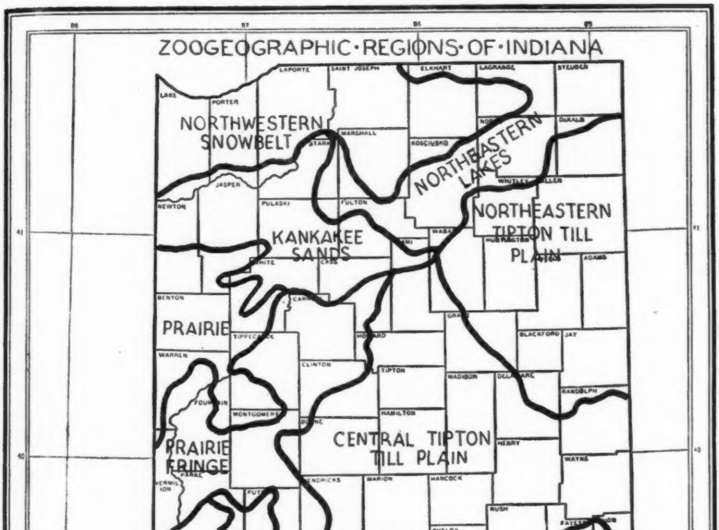


Fig. 1.—Outline map of Indiana

There is an annual average rainfall of around 40 inches, with 45, 40, and 35 inches in southern, central and northern Indiana, respectively. Snowfall in these three sections average 15, 20, and 40 inches, respectively.

*Northwestern snowbelt region.*—This area, extending from Lake County on the west to Elkhart County on the east, is greatly affected by the moisture-laden winds from Lake Michigan. The amount of snowfall, especially in the vicinity of the Valparaiso Moraine, is the greatest in the state. A total of around 50 inches is normal, and the ground is snow covered from 50 to 60 days in the winter.

Most of this region comprises lacustrine plains which formerly contained broad marshes, broken up by low sand ridges and interspersed with higher morainic deposits.

The region is highly populated as a result of industrialization. Heavy hunting pressure, coupled with adverse climate result in below average bags of most upland game species (Barnes, 1946). Ruffed grouse, once a common inhabitant (Leopold, 1931), have disappeared with the exception of one report from Elkhart County in 1942. Up until recent years prairie chickens have also existed in the burr oak openings to the east, and their former habitat now supports some Hungarian partridges. The heavy snowfall is not conducive to good quail populations. Butler (1897) noted that hard winters greatly reduced their numbers in this section of the state. The infrequent occurrence of hickory and beech in the predominant oak woodlots ( Deam, 1940) causes more abnormal fluctuations in squirrel populations due to mast failures. Squirrel hunting is often poor. Rabbits are taken in below average numbers, particularly in the western portion. Along with the usual fur-bearers (Lyon, 1936), trappers occasionally report a badger catch. Waterfowl, especially geese, stop during fall migrations. Flocks of mergansers and various diving ducks may be seen on Lake Michigan during the entire winter period.

*Northeastern lake region.*—This body of land begins in Steuben County in the northeastern corner of the state and extends in a southwesterly direction into Fulton and Marshall counties. Snowfall is somewhat lighter than to the northwest. Potholes, marshes, lakes and streams offer better edge cover. The rolling terrain cuts the landscape up into smaller fields with more diversified farming.

Rabbits are taken here in average numbers for northern Indiana. Due to greater interest in fishing at the time when the squirrel season is open, the bag remains low. Pheasants are established over the entire region, while Hungarian partridges are found in scattered areas of level farm land. Quail hunting is fairly good for this part of the state. Muskrat trapping is at its best and night hunters enjoy about average catches of raccoons. Ducks and geese stop on the lakes and streams, but it is off the main migratory route. Evermann and Clark (1920) describe the slaughter of coots on Lake Maxinkuckee at the turn of the century. Coot hunting remains a popular sport on many of the larger lakes today.

*Kankakee sand region.*—During the glacial period, the Kankakee Basin was inundated by melting ice water that carried a sedimentary fine sand. In the

winter, this flood water ceased and the prevailing winds from the northwest built up islands of sand dunes, particularly on the south side of the Kankakee River.

This creation by nature, along with the numerous dredge ditches, contributes toward an above average quail population for northern Indiana. Pheasants are also found in numbers similar to the lake region. In Newton County, prairie chickens are making their last stand on the submarginal farm land still remaining in grass. The sandy soil of this region is disliked by Hungarian partridges and evidently acts as a barrier to the western extension of their range. Squirrel populations fluctuate the same as in the Northwestern Snowbelt Region. Rabbits are also below average. Originally, this region embraced the Grand Marsh, comprising some one-half million acres renowned for its waterfowl. Although it is now drained and the flight has shifted to the west, it still provides waterfowl shooting. Trapping for aquatic fur-bearers is good, but night hunting is only fair.

*Prairie region.*—This area was formerly covered with prairie grass typical of the Great Plains section of the United States. The fertile soil is subjected to a high degree of cash grain agriculture with little native cover for upland game, except along Osage-orange fencerows and brushy borders that have not yet yielded to the axe and bulldozer.

Benton County has one of the highest fertility ratings in the state and, even though it is devoid of cover, pheasant hunting is generally good here. A few reports have been received of Hungarian partridges in Warren and Tippecanoe counties. Quail, rabbits, squirrels, and other species of wildlife are all limited by poor cover conditions. Excluding a few remnant birds, the prairie chicken, which was originally abundant (Miles, 1913), has been eliminated by destruction of grassland.

*Prairie border region.*—With the exception of a narrow border strip, this particular habitat lies on the east side of the Wabash River. It is located within an older glaciated section that has been more deeply dissected by waterways that drained old upland swales. It is characterized by silt loam soils, some of windblown origin (Bushnell, 1944). The land is generally rolling and lower in productivity than the regions to the east and west. There is less corn and more hay and pasture, especially in the southern portion.

The river bluffs along the Wabash and tributary streams offer good habitat for wildlife. In all regions previously mentioned, the fox squirrel is the only animal usually found by squirrel hunters, but here, the gray squirrel begins to show up in the river bottoms.

Quail hunting is fairly good for northern Indiana with the southern section having the highest average. Pheasant populations are relatively light. It provides the best rabbit and squirrel habitat in the northern part of the state. Some waterfowl hunting occurs along the larger streams, and the wooded bottoms support a good raccoon population.

*Central Tipton till plain region.*—The land within this territory may be described as a gently rolling fertile plain created by till material resulting from glacial action. It is noted as a grain and livestock section. Like the prairie area, the intensive agricultural practices limit habitats for wildlife. The soil

is inherently rich and more cover would greatly increase its wildlife carrying capacity. Hunting pressure is very heavy.

Rabbits, fox squirrels, and quail offer fair to good sport in the western and southern section but decrease to the east. Conversely, the Hungarian partridge in this eastern section provides some of the best hunting for this bird in the state. Pheasants are light.

*Northeastern Tipton till plain region.*—The origin and general characteristics of this region are quite similar to those of the previously described section on the west. However, the parent material and subsoils are heavier, thus affording poorer drainage and somewhat less favorable agricultural conditions. A more general type of farming is practiced. This region has the most uniform distribution of Hungarian partridges, but ranks with the Northwestern Snowbelt Region as the poorest habitat for quail. It supports more pheasants than the Central Tipton Till Plain Region. Fox squirrel hunting is generally poor, while rabbits are average for northern Indiana.

*Wabash lowland region.*—The lower Wabash River region may be described as that portion of southern Indiana lying between Illinois on the west and the hill section on the east. It is characterized by broad river valleys and adjoining soils of windblown origin. Valley slopes near the larger rivers are predominantly sands of coarse texture. With increase of distance to the east and gain in elevation, the soil texture becomes finer and of a silty nature. Thus, this region may be understood as quite diversified from a landuse standpoint, varying from river bottom corn to truck crops and orchards on the sand to more general agricultural and strip mine operations elsewhere.

In this region, as well as the others to be discussed in southern Indiana, the pheasant has not been successfully established. Localized areas exist in river valleys where some shooting could be provided under an expensive restocking program. Here, quail hunting is the best in the state. Rabbits also provide very good sport, but decline in the counties bordering the Ohio River. Fox squirrels over the entire area and gray squirrels in the river bottoms offer fair to good shooting. Fur-bearer trapping is good. Like all other regions in southern Indiana, opossums are taken in higher and muskrats in lower numbers than in the north. Night hunting for raccoon is good. Along the Ohio River and the lower reaches of the Wabash River, waterfowl winter in numbers dictated by fluctuating weather conditions. Here they provide the best shooting in the southern part of the state.

*South-central hill region.*—For the most part, this section comprises the unglaciated part of the state. It may roughly be divided into three areas, the Crawford Upland on the west and the Norman Upland on the east. In between these two ranges of sandstone hills lies the lower Mitchell Plain, broken up by general farming, sink holes and building stone quarries. The uplands contain a high proportion of woodland, interspersed by ridge and valley crop land.

Much of the territory is often referred to as submarginal for farming, but the same reference cannot be made to quail, with good average kill returns from most parts of this region. A remnant ruffed grouse population can still be found in scattered localities in the Norman Upland.

Unlike other parts of the state, the gray squirrel comprises over 40 per cent of the total bag, and hunting for these animals is at its best here. Likewise, the gray fox is taken in about equal percentages with the red fox. Hunting for rabbits may be generally considered as poorer than in the regions to the east and west. As a result of restocking white-tailed deer during the last 15 years, the herd is now estimated at 4,000 animals, and shows evidence of increasing each year, except in localities where poaching and dogs are exerting adverse influences.

*Southeastern lowland and flats region.*—This region contains two distinct geographic areas. The Scottsburg Lowland is a broad, rolling expanse of low elevation, being bordered on the west by the Knobstone hills and on the east by a higher plateau locally called the "Flats." This last mentioned area has extensive level farm land on the divides draining into the Muscatatuck River. The claypan under the surface causes poor drainage of the acid soil.

Both the "Lowland" and the "Flats" provide some of the best quail habitat in the state. Rabbits and squirrels are found in above average numbers. Fox hunting and chasing reaches its highest popularity here.

*Dearborn upland region.*—The Dearborn Upland lies within the drainage basin of the Whitewater River. The narrow, winding ridge-tops are dissected by steep slopes bordering small stream valleys. This region may be called the tobacco country of Indiana. Much of the land is also devoted to the pasturing of dairy cattle.

Although hunting can be considered as relatively light, quail hunting is poorer than in other parts of southern Indiana. Extensive pastures and wooded side hills are not too productive for quail. Rabbits are taken in below average numbers for the south, while squirrel hunting may be described as good.

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# The Vegetation of the Jackson Hole Wildlife Park, Wyoming[1]

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The Jackson Hole Wildlife Park is located near Moran in Teton County, Wyoming. It was established in 1947 and is now stocked with a variety of big game animals, including antelope, bison, deer, elk (wapiti), and moose. The Park serves as a center for the study of the biota of the region.

The purpose of botanical work in the Park is threefold: (1) to determine the nature of the vascular flora; (2) to describe the plant communities; (3) to learn the effect of the big-game animals on the vegetation. This report is concerned mainly with the nature of the vascular flora, but qualitative descriptions of the major plant communities as well as a generalized account of the climate, topography, and soils of the area are also included.

Four seasons have been given to collecting and cataloguing the vascular plants of the Park.[2] An herbarium has been established at the Laboratory of the Jackson Hole Station for Biological Research near Moran. Duplicates of the collections are on file at the Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyoming.

## General Features of the Area

### Location and Size

The Jackson Hole Wildlife Park lies in the northern portion of Jackson Hole in Teton County, Wyoming (latitude 43° 52′ N; longitude 110° 35′ W). It consists of about 1400 acres of land, most of which lies north of and immediately adjacent to the Snake River. The Park is about six-tenths of a mile wide from north to south and two and seven-tenths miles long from east to west. It is very irregular in shape because of the tortuous course of the Snake River which forms most of its southern boundary.

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1 Contribution number 218 from the Department of Botany and the Rocky Mountain Herbarium of the University of Wyoming. The project was supported jointly by the University of Wyoming and the Jackson Hole Wildlife Park.

2 The valued assistance of each of the following in helping to resolve some of the taxonomic problems is gratefully acknowledged: C. L. Porter and A. A. Beetle of the University of Wyoming; C. R. Ball, formerly of the United States Department of Agriculture; G. J. Goodman of the University of Oklahoma; A. J. Cronquist of the State College of Washington; and my wife, Mildred Stites Reed.

## TOPOGRAPHY AND RECENT GEOLOGICAL HISTORY

Although near the rugged Teton Mountains which lie to the west across Jackson Lake, there is little relief within the Park itself. Its average elevation is approximately 6750 feet above sea level.

The hills which lie along the northern boundary of the Park represent the drift-covered base of North Hill (Unnamed Butte). Along the south side of the Snake River a very slight protrusion of the base of Signal Mountain into the Park results in some steep slopes. The bases of both North Hill and Signal Mountain became the resting places of quantities of till during the Pleistocene glaciations.[3]

As its former channel became blocked by glacial deposits, the Snake River established its present course by cutting eastward through the moraine of the Jackson Lake Glacier. In postglacial time the activities of the river have resulted in flood plains, terraces, and alluvium-covered meadowlands which collectively constitute most of the Park. The higher terraces are more than twenty feet above the present level of the river, while the meadowlands and lower terraces occur at varying levels beneath. There is a limited expanse of flood plain still under the influence of the river, especially around the margin of the several small islands in the river. The level of the Snake is artificially controlled by a dam at the point where it leaves Jackson Lake. Streamflow is determined by demands for irrigation downstream. This situation often results in untimely fluctuations of the water level, to which the biota adjacent to the channel adjusts with difficulty, if at all.

Pacific Creek flows along the easternmost edge of the Park as it approaches its confluence with the Snake River. The present bed of Pacific Creek has been formed by post-glacial down-cutting through the gravel deposited by the Jackson Lake Glacier. A well-defined terrace borders the Creek, and a cobbly strand with occasional shifting sand- and gravel-bars characterizes its bed immediately adjacent to the channel.

Two small ponds occur within the Park. Both are spring-fed, shallow, and with mucky bottoms. A rich vascular flora is properly disposed about their margins.

At the extreme western edge of the Park the land is flat and poorly drained. This area is a portion of an outwash plain of the Jackson Lake Glacier that has not been affected by the recent activities of the Snake River, except where the river is entrenched some fifteen to twenty feet within it and the raw glacial detritus is thus exposed in practically vertical section.

## CLIMATE

Weather records have been kept since 1911 at nearby Moran.[4] Especially significant features of the climate are the long cold winters, the deep snow, the short growing season, and the low mean annual temperature.

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3 References to glacial history are all drawn from the excellent article on the glaciation of the region by Fryxell. Fryxell, F. M. 1930. Glacial features of Jackson Hole, Wyoming. Augustana Library Publication 13. 129 pp. Map.

4 1947-Meteorological Summary, Moran, Wyoming. U. S. Dept. of Commerce, Weather Bureau. 5 pp. mimeo.

The average temperature for the period from May through August is approximately 51 degrees Fahrenheit. The mean annual temperature is 34.3 degrees Fahrenheit. Temperatures between minus 40 and minus 50 degrees Fahrenheit are not uncommon during the winter months. A minimum temperature of minus 63 degrees Fahrenheit was recorded in February of 1915. Frosts may occur at any time during the year. The average length of the frost-free period is approximately sixty days.

Snowfall has been recorded in every month of the year, although the amount occurring in June, July, and August is negligible. The mean annual snowfall is 136.9 inches. The mean annual precipitation is slightly more than 21.5 inches. Practically all of the precipitation from November through April is in the form of snow.

A climograph which summarizes the variations in both mean monthly temperature and mean monthly precipitation is presented in Figure 1. These data were procured at the Moran Weather Station and represent averages for the years from 1911 through 1947. It is apparent that July is the month when the highest mean monthly temperature coincides with the lowest mean monthly precipitation. Over the years the amount of precipitation fluctuates between 2.3 inches in January and 1.2 inches in July, but on the whole it is remarkably evenly distributed throughout the year.

Most of the area included within the boundaries of the Park was assigned to the Transition Life Zone by Cary in 1917.[5] Thornthwaite assigned the region to the subhumid climatic category.[6] The region falls within the Montanian biotic province.[7]

## SOILS

No detailed descriptions of the soils of the Jackson Hole region have been published. On a generalized map of the Wyoming soil groups[8] the soils of the Jackson Hole Wildlife Park have been classified mainly as brown bench loams and bottom soils and have been called Laurel Soils. All of the soils observed within the Park appear to be quite immature. They differ markedly from one vegetational type to another.

The soil which is developing upon the glacial till along the base of North Hill is very stony and quite lacking in profile development. Sagebrush (*Artemisia tridentata*) occurs as a dominant on this type where the slope is steep and the exposure toward the south. Small clumps of aspen (*Populus tremuloides*) characterize somewhat moist sites, and a coniferous forest occurs on the north slope of Signal Mountain coincidental with the till. Steep slopes and the coarse parent material make this sort of site exceptionally well drained.

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5 Cary, M. 1917. Life Zone Investigations in Wyoming. U. S. Dept. Agr., Bur. Biol. Survey, N. A. Fauna 42:1-95.

6 Thornthwaite, C. W. 1940. Atlas of Climatic Types in the United States. 1900-1939. U. S. Dept. Agr. (S.C.S.) Misc. Pub. 421.

7 Dice, L. R. 1943. The biotic provinces of North America. 78 pp. University of Michigan Press, Ann Arbor.

8 Dunnewald, T. J. 1934. Wyoming Soil Groups Map, personal copy from Department of Soils, University of Wyoming, Laramie, Wyoming.

The soil on that portion of the outwash plain of the Jackson Lake Glacier which lies within the Park is developing under the influence of a very high water table. It is very dark in color and essentially azonal. Such a soil in this region supports subclimax vegetation, main willows (*Salix* spp.), sedges (*Carex* spp.), grasses, and a variety of moisture-preferring forbs.

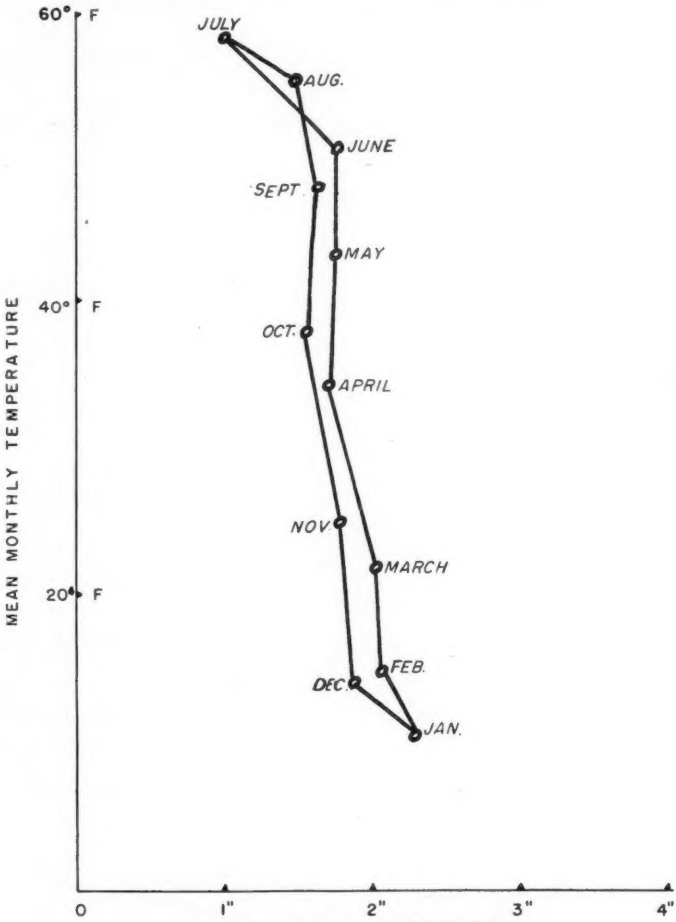


Fig. 1.—Climograph for Moran, Wyoming. The means for each month are based on data accumulated from 1911 through 1947, inclusive.

The soils of the broad meadowland and of the terraces along the watercourses are underlain by deep deposits of sand and gravel. A variety of plant communities occupy these sites. The extent to which the soil profile is differentiated appears to depend largely on the degree to which the site has been free from such disturbing factors as alluviation, cultivation, fire, or grazing.

The absence of a marked layer of calcium in the profiles of the soils beneath grasses and sagebrush is noteworthy. This fact is undoubtedly due to the combined effects of a relatively high mean annual precipitation and good drainage.

Instability and immaturity characterize the solum which is only sporadically exposed about the margins of the ponds and the shifting bars of sand and gravel in the streambeds. Such sites support a variety of vascular plants.

## PREVIOUS USE

The Jackson Hole Wildlife Park includes portions of five original homesteads, all of which may have had different types and degrees of use for varying periods of time. Grazing by livestock and fire must both be assumed to have been disturbing factors since the time of settlement. Although the type and extent of use is not intimately known, it is apparent that no virgin conditions existed there when the Park was established.

Ninety-five percent of the land within the boundaries of the Park was retired from intensive agricultural use between November, 1929 and May, 1931, some sixteen to eighteen years prior to the establishment of the Park. The remainder of the land has not been used for agricultural purposes since 1947, except for the harvesting of hay near the western edge of the area and some indiscriminate grazing of unfenced portions by riding horses from an adjacent lodge.

Old stumps in various stages of decay bear witness to repeated removal of timber trees over the many years since settlement. Fire scars on the butts of the older trees as well as most of the stumps are not uncommon.

It is quite impossible to evaluate the extent to which the Park has been used by the huge elk herd that winters on the Federal Elk Refuge near the town of Jackson, Wyoming, some thirty miles to the south. The migrant portion of the herd has undoubtedly had some influence on the vegetation of the area, since one of the principal paths which it uses passes directly through the Park.[9]

## THE PLANT COMMUNITIES

The variety of plant communities which comprise the vegetation of the Jackson Hole Wildlife Park is in part a reflection of the geological history of the area. The effect of exposure is clearly demonstrated by the occurrence of aspen and sagebrush communities on south- and southeast-facing slopes in contrast with the lush coniferous forest which covers north- and northwest-facing slopes, and this in spite of the fact that each type of site is underlain

[9] Blunt, F. M. 1950. Migration study of the Jackson Hole elk herd. Wyoming Wildlife 14:25-32.

by similar till deposited by the glacier as a unit mass. Local variations in the depth of the water table beneath the surface of the ground produces pronounced differences in vegetation within very small distances. The previous use of the land has clearly left its imprint on the present vegetational mosaic within the Park. Extensive meadows occur and these are dominated by several species of exotic grasses, even after years of agricultural disuse. Among biotic agents, other than man, the beaver is outstanding with respect to its effect on both site and vegetation.

In the following pages the major plant communities are designated and briefly described. Finally, a list of the vascular plants of the Park and its immediate vicinity is presented together with information concerning the occurrence and the abundance of each species in the various communities.

## Aquatic Communities

Aquatic plants abound in the natural ponds, and the ponds behind beaver dams, in the backwater of the Snake River, and in some of the small streams. These plants fall naturally into the following categories: (1) submerged aquatics—e.g., *Ranunculus aquatilis, Potamogeton* spp., and *Utricularia vulgaris;* (2) free-floating hydrophytes—e.g., *Lemna minor* and *L. trisulca;* (3) rooted hydrophytes with floating leaves—e.g., *Nuphar polysepalum* and *Ranunculus natans;* and (4) rooted emergent hydrophytes—e.g., *Carex* spp.. *Glyceria* spp., and *Sium suave.*

## The Community on Mud

Numerous muddy banks and mud-covered depressions occur in the Park. Each of these is of limited extent and most of them are sporadically flooded. Their vegetative cover represents a stage in the hydrosere which follows the true aquatic communities and precedes the sod-forming stage later in the sere.

Two types of plants occur on the mud. On the one hand are those truly amphibious plants which are capable of adjusting themselves to the absence of standing water—for example, *Callitriche palustris, Polygonum amphibium,* and *Porterella carnosula.* On the other hand, there is a group which flourishes on mud and also persists as a part of the sod-forming community. The latter are the terrestrial pioneers and include, among others, *Alopecurus aequalis, Eleocharis acicularis, Juncus* spp., *Equisetum arvense,* and three species of *Veronica.* These two groups form a loosely knit community that shows considerable variation in composition from one place to another.

## The Sod-forming Community near Open Water

Near the edge of quiet water where neither active erosion nor deposition is occurring, there is a community in which sedges predominate. This community forms a very tightly packed sod, and the effect of such firmly interwoven masses of roots and rhizomes is to stabilize the site against erosion in times of high water. Occasionally such sod-forming communities do become undermined by running water, following which some portions may persist as remnants overhanging deepened channels for many years. Normally, how-

ever, more mesophytic species invade these dense sods and thus continue the development of the hydrosere. Especially prominent in the sod-forming community are many plants which may also be found as regular components of several other communities. The dominant sedges include *Carex lanuginosa, C. nebraskensis, C. occidentalis,* and *Eleocharis macrostachya.* The rush, *Juncus balticus,* and the grasses, *Glyceria elata* and *Poa annua,* are prominent, as are the following forbs: *Epilobium adenocaulon, Mentha canadensis,* and *Scutellaria galericulata.*

## THE MEADOWS

Two types of true meadow vegetation occur within the Park, one of which will be designated as the sedge meadow community, and the other as the sedge-grass meadow community. The sedge meadow community is apparently the next stage in the hydrosere beyond the sod-forming community just described. In turn, the sedge meadow community is superseded by the sedge-grass meadow community.

The sedge meadow community is underlain by a very firm sod and is often covered for prolonged periods during the growing season by standing water to a depth of several inches. Five species of sedge (*Carex* spp.) are especially prominent in this community. The grasses are represented by a few scattered individuals, mostly *Alopecurus aequalis* and *Hordeum brachyantherum.* The conspicuous forbs, *Dodecatheon pauciflorum* and *Gentiana thermalis* are abundant along with three species of the genus *Equisetum.*

Wherever the peculiarities of micro-relief have resulted in mounds, or even slightly elevated areas, the sedge meadow community gives way to the sedge-grass meadow community, in which both sedges and grasses occur as dominants. The four sedges (*Carex* spp.) are different species from those of any of the wetter habitats. The dominant grasses include *Agropyron trachycaulum, Agrostis hiemalis, Bromus inermis, Deschampsia caespitosa, Melica spectabilis, Phleum pratense,* and *Poa palustris.* About thirty species of forbs occur, notable among which are the clovers (*Trifolium* spp.). This latter community is extremely productive of a good variety and yield of forage.

## THE SHRUB-SWAMP COMMUNITY

On sites where the water table is very near the surface of the ground but where previous vegetation has produced a considerable degree of stability, the shrub-swamp community occurs. It is represented in the Jackson Hole Wildlife Park by a number of disjunct stands. Each stand is an irregular aggregation of shrubs, mostly willows (*Salix drummondiana* var. *subcoerulea, Salix geyeriana, Salix pseudocordata,* and *Salix wolfii*). The dispersion of the units of this community varies to the extent that frequently one isolated clump of willows occurs amidst several acres of meadowland, or at the opposite extreme, the willows form a nearly closed canopy which precludes the development of the meadow vegetation. The shrub-swamp community has reality only where the dominance of the willows is such as to exclude a representative expression of any of the contiguous communities. The reduced light intensity under the canopy formed by the shrubs coupled with the abundant mois-

ture which the site ordinarily provides favors the abundance and vigorous growth of a great variety of forbs and grasses. Conspicuous and common grasses of this community include *Bromus ciliatus, Calamagrostis canadensis, Calamagrostis inexpansa, Poa leptocoma,* and *Poa pratensis.* Among the characteristic and more conspicuous forbs are *Aconitum columbianum, Aster integrifolius, Castelleja* spp., *Galium boreale, Geranium nervosum, Hydrophyllum capitatum, Ranunculus* spp., and *Smilacina stellata.*

## The Communities of Cobbly, Gravelly, and Sandy Streambeds

Much of the wide bed of Pacific Creek at the eastern edge of the Park is made up of gravel and sand bars. The channel of the stream shifts considerably within its banks from year to year, leaving new exposures of gravel, sand, and cobble stones after each period of high water. Cobbly pavements occur locally along the Snake River as well. Upon such sites the early stages of colonization and vegetational development occur.

The most recently deposited sands and gravel support a sparse and scattered plant cover. The species that occur are, nevertheless, numerous and varied. The areas covered with cobblestones support an even sparser vegetative cover. On such unstable sites within the streambeds the rushes are conspicuous, especially *Juncus bufonius, J. ensifolius, J. longistylis, J. parryi,* and *J. saximontanus.* The grasses, *Muhlenbergia andina* and *M. filiformis* occur regularly along with *Alopecurus aequalis* and *Hordeum brachyantherum.* More than fifteen species of dicotyledonous forbs are also present. The horsetails are common and abundant, including *Equisetum arvense* and its variety *alpestre, E. laevigatum,* and *E. variegatum.*

On the more stable and elevated areas within the streambeds, where aggradation occur only under extreme flood conditions, certain willows (*Salix caudata* and its variety *bryantiana, S. drummondiana* var. *subcoerulea, S. mackenziana,* and *S. melanopsis* with its variety *tenerrima*), the mountain alder (*Alnus tenuifolia*) and the narrow-leaf cottonwood (*Populus angustifolia*) dominate a community which includes a heterogeneous variety of dependent plants. Conspicuous clumps of both red osier (*Cornus stolonifera*) and silverberry (*Elaeagnus commutata*) occur along the streambanks either contiguous with the willows or standing quite apart. Such common weeds as *Chenopodium album, Lactuca integrata,* and *Lepidium perfoliatum* find footholds in this situation, along with a dozen or more species of grasses and about thirty other forbs. No one species is exceedingly abundant. This community represents an intermediate stage between that found on raw alluvium and the streamside forest of the adjacent terrace.

## The Streamside Forest

The post climax forest of the region occurs a few feet above normal flood level on the first terrace above Pacific Creek. Narrow-leaf cottonwood is the major dominant. Amongst the larger and older cottonwoods, where optimum moisture conditions prevail throughout the growing season, there are scattered clumps of blue spruce trees (*Picea pungens*). Pure stands of the latter do

not occur within the Park, but nearby there are similar terraces near streams where blue spruce is the major dominant. In other situations of a comparable nature, such as the region along Pilgrim Creek about five miles from the Park, balsam poplar (*Populus balsamifera*) shares dominance with narrow-leaf cottonwood and blue spruce.

The relationship of the streamside forest to the vegetation on the more stable sites within the streambeds is clearly evident. When sufficient aggradation has occurred, or when the active channel of the stream has withdrawn, the willow thickets which had withstood repeated flooding for many years are invaded by narrow-leaf cottonwood. In turn the cottonwood assumes dominance and as the willows become sparser the characteristic shrubs, forbs, and grasses of the streamside forest appear. Certain shallow depressions which have remained on the terraces for many years continue to be occupied by the willows and their subordinate vegetation. All of the species of willow that occur within the streambed persist on the wetter portions of the terrace, but in addition several other species of this genus (*Salix geyeriana, S. lutea, S. pseudocordata,* and *S. wolfii*) enter and become a part of the community. Together the various species of willows constitute a complex aggregation which not only serves to shelter the young cottonwoods, but which also remains as an understory to the cottonwoods as the latter assume a dominant role. Other conspicuous and common shrubs are the russet buffaloberry (*Shepherdia canadensis*), gooseberries and currants (*Ribes* spp.), the rose (*Rosa woodsii*), and honeysuckle (*Lonicera involucrata*).

On the most remote portions of the terraces, farthest from the streambed, the streamside forest ends abruptly, and contiguous stands of either big sagebrush (*Artemisia tridentata*), silver sagebrush (*A. cana*), aspen (*Populus tremuloides*), or lodgepole pine (*Pinus contorta*) occur. Both lodgepole pine and aspen have been found within the streamside forest, but neither are important species there.

Over sixty species of forbs have been found within the streamside forest, ranging from the delicate and scarce fairy's slipper orchid (*Calypso bulbosa*) to the equally delicate but exceedingly abundant shooting star (*Dodecatheon pauciflorum*), or larkspur (*Delphinium nelsoni*). Gentians (*Gentiana* spp.), composites (*Achillea millefolium, Antennaria* spp., *Aster* spp., *Erigeron* spp., *Helianthella quinquenervis, Solidago* spp.), and legumes (*Astragalus* spp., *Medicago lupulina, Oxytropis deflexa* and its variety *sericea,* and *Trifolium rydbergii*) are among the most important forbs present. About twenty species of grasses occur in this community, including members of the genera *Agrostis, Agropyron, Bromus, Calamagrostis, Danthonia, Deschampsia, Festuca, Glyceria, Hierochlöe, Hordeum, Koeleria, Muhlenbergia, Phleum, Poa,* and *Stipa.*

## THE INTERVALE VEGETATION

Closely akin to the site upon which the streamside forest occurs is a grass-covered intervale that lies on a broad terrace about ten feet above the channel of the Snake River. This intervale is no longer subject to inundation, since the flow of the river is completely controlled by a dam a short distance upstream. The intervale is crossed by a series of abandoned irrigation ditches.

For many years this area was used for the production of hay, and at the present time it is nearly completely enclosed by a fence to retain the big-game animals for display during the tourist season.

Except for its very periphery, the intervale is dominated by grasses, both native and exotic. Various portions are separately dominated by red top (*Agrostis alba*), timothy (*Phleum pratense*), and smooth bromegrass (*Bromus inermis*). The vegetation associated with each of these dominants is so characteristic that it becomes necessary to consider each dominant as marking a discrete subdivision of the grass-dominated community of the intervale when intensive phytosocial or grazing studies are made.[10] In addition to the grass species already mentioned *Agropyron subsecundum* and *A. trachycaulum, Agrostis hiemalis, Deschampsia caespitosa, Hordeum brachyantherum Poa canbyi, P. fendleriana,* and *P. pratense,* and *Stipa columbiana,* and *S. lettermani* also occur. It is further characterized by its rich herbaceous flora of nearly seventy recorded species. The common dandelion (*Taraxacum officinale*), the gentian (*Gentiana forwoodii*), the larkspur (*Delphinium nelsoni*), cinquefoils (*Potentilla* spp.), clover (*Trifolium rydbergii*), and the buttercups (*Ranunculus* spp.) are very common and conspicuous members of the intervale vegetation.

A narrow portion of the intervale along the river has been invaded by silver sagebrush (*Artemisia cana*) and shrubby cinquefoil (*Potentilla fruticosa*). In the course of a few years these shrubs are capable of exerting much influence and of spreading rapidly into the adjacent grassland. Other peripheral vegetation includes a few widely spaced aspen trees on the steep slope of one of the higher terraces and a willow thicket on a particularly poorly drained site.

The soil of the intervale shows considerable local variation in both its texture and the degree to which it is drained. Some of the shallow depressions remain quite wet until the growing season is well advanced. The drier portions have coarse, gravelly soils and are exceptionally well drained.

Irrigation is no longer practiced. Late summers and early fall droughts are undoubtedly of considerable significance in determining the nature of the intervale vegetation.

## THE SILVER SAGEBRUSH COMMUNITY

On several disjunct areas within the Park silver sagebrush is a conspicuous dominant. The community in which it occurs is invariably near a watercourse, and thus it receives a more regular supply of soil moisture than does the big sagebrush community which it superficially resembles. Not uncommonly these sites are distinctly wet in spring and early summer.

The silver sagebrush community is capable of invading abandoned hayfields. It occasionally gives way to aspen as vegetational development occurs. Quite frequently small clumps of silver sagebrush are found at the edges of willow thickets, but in such positions they hardly form discrete communities.

Silver sagebrush is almost always the sole dominant in the community bearing its name, an occasional big sagebrush plant or a scattering of shrubby

10 Reed, J. F. 1950. The meadows of the Jackson Hole Wildlife Park. Jour. Colorado-Wyoming Acad. Sci. 4:53.

cinquefoil (*Potentilla fruticosa*) about its periphery being the only exceptions noted. Nearly a score of grass species have been found in this community, of which the bluegrasses (*Poa canbyi, P. interior, P. pratensis*), june grass (*Koeleria cristata*), the needle grasses (*Stipa columbiana* and *S. lettermani*), and the brome grasses (*Bromus anomalus* and *B. carinatus*) are especially important. More than forty species of forbs regularly occur with the cinquefoils (*Potentilla arguta* and *P. flabelliformis*) very common along with *Aster integrifolius, Campanula rotundifolia, Linum lewisii, Lupinus parviflorus,* and *Sieversia ciliata.*

## THE ASPEN COMMUNITIES

Even casual observation suggests the existence of two distinct types of aspen-dominated communities within the Jackson Hole Wildlife Park. On the one hand, there are relatively open aspen stands on the xeric hillsides, and on the other, the densely shaded aspen groves of the flatter terrain.

Irregularly shaped stands or narrow strips of aspen occur on the slopes of the till-covered hills. These are a conspicuous feature of the landscape in the region of the Park. Such sites are among the most arid of the region, especially during midsummer and early fall. The underlying soil is normally coarse; yet in time it comes to exhibit a distinct mull type of humus and several inches of dark A horizon in which there is a considerable proportion of small particles. These stands occur on an exposure which is generally toward the south and upon a site with sufficient slope for rapid drainage.

On the more level sites adjacent to meadows or swamps are the aspen groves which are characterized by closed canopies, dense shade, moist subsoil, and a very lush growth of shrubs, forbs, and grasses. Except for the conditions that prevail in the spruce-fir communities, the environment of these aspen groves appears to be as mesic as any encountered in the forest communities of the region. Although the soil is never so completely saturated as in certain adjacent shrub-swamps, very moist conditions prevail early in the growing season, and later the soil moisture supply dwindles during the summer and early fall. A well-developed mull type of humus characterizes the soil of the aspen groves, the A horizon is much deeper than that on the hillsides, and in the cases examined medium fine sand constituted the underlying parent material in the groves.

The two types of aspen-dominated communities differ markedly from a floristic viewpoint. Within the hillside type only thirty-eight species of vascular plants have been found, whereas the aspen groves on the moist flats have yielded a total of seventy-eight species. Douglas fir (*Pseudotsuga taxifolia*) is an occasional invader of the hillside aspen stands, but no conifers have been found within the groves. The western chokecherry (*Prunus melanocarpa*) is a constant component of the aspen stands on the hillsides where it serves as an understory beneath and between the characteristically widely spaced aspen trees. It is conspicuously lacking in the aspen groves in moist sites, but the number and diversity of other species of shrubs is equally characteristic of this type of stand. Eleven species of shrubs have been found in the aspen groves on moist sites and only four species on the dry hillsides. There is

more than double the number of forbs on moist sites as compared to dry, and nearly twice as many species of grasses. It seems logical to consider the aspen communities of the Park as two entities because of the outstanding differences in both floristic composition and in the nature of their sites.

Among the larger and more conspicuous forbs of the hillside aspen stands are *Agastache urticifolia, Balsamorrhiza sagittata, Erigeron speciosus, Geranium nervosum*, and *Viguiera multiflora*, all of which are lacking in the moist aspen groves. The stands have many species of conspicuous forbs in common, for example, *Aster integrifolius, Helianthella quinquenervis, Lupinus parviflorus, Osmorhiza obtusa* and *O. occidentalis, Perideridia gairdneri, Senecio serra*, and *Valeriana occidentalis*. Especially prominent forbs found in the aspen groves on moist sites, but absent from the stands on the hillsides, are *Angelica pinnata, Delphinium occidentale, Epilobium angustifolium, Hackelia diffusa*, and *H. floribunda, Ligusticum filicinum, Pedicularis paysoniana, Rudbeckia occidentalis, Smilacina stellata, Thallictrum fendleri* and *T. occidentale*, and *Valeriana obovata*.

## THE BIG SAGEBRUSH COMMUNITY

The most widespread and conspicuous of the plant communities of the entire Jackson Hole region is the big sagebrush community. It covers many square miles of outwash plains, abandoned terraces, and till-covered hillsides throughout the Hole, but in the Park it occurs mainly on the till which covers the flanks of North Hill.

The big sagebrush community is an enduring one, invaded only by an occasional lodgepole pine or by sprouts from adjacent aspen stands. There is constant conflict between the big sagebrush community and the hillside aspen community. Advances of each of these into the other is continuously occurring, and any success is probably correlated with whatever coincident alternation of wet or of dry seasons there may be. The result of this interplay is virtually a stalemate in the vicinity of the Park, as attested by the dead aspen sprouts a few yards out in the sagebrush and the depauperate or dead sagebrush within the aspen canopy. Whether it be aspen or lodgepole pine invasion, it appears that both climatic and edaphic conditions favor the persistence of the big sagebrush community as a major element in the vegetation of the region.

The soil profile of the big sagebrush community is not particularly well differentiated on the whole. On comparatively level sites, however, the litter accumulates to the extent of an inch or slightly more in depth, the A horizon is a few inches deep and consists of a brown fine-sandy-loam, and the thin B horizon is a yellowish coarse-sandy-loam. All this is normally underlain by a very coarse gravelly and stony mass of parent till, ten or more feet deep. The entire soil mass has a large proportion of coarse gravel throughout its vertical extent. Surface erosion may produce a gravel pavement on localized areas, although this is not the common condition encountered.

Floristically this community is characterized by a rich assemblage of growth forms. Seven species of shrubs occur as integral components of the

community. Big sagebrush is clearly the controlling dominant in almost all instances. Only antelope brush (*Purshia tridentata*) and threetip sagebrush (*Artemisia tripartita*) exert anything approaching codominance with the big sagebrush, and this situation prevails only in rather localized areas. Silver sagebrush sometimes encroaches upon the margin of the big sagebrsuh community. Sarvisberry (*Amelanchier alnifolia*) occurs as scattered clumps in certain restricted portions of the community. Oregon grape (*Mahonia aquifolium*) and snowberry (*Symphoricarpos tetonensis*) are both common but subordinate shrubs. The grasses are represented by some twenty or more species which contribute significantly to the ground cover beneath the shrubs. The wheat grasses (*Agropyron* spp.), the brome grasses (*Bromus* spp.), fescue (*Festuca idahoensis*), june grass (*Koeleria cristata*), *bluegrasses* (*Poa* spp.), and needle grasses (*Stipa* spp.) are especially abundant and important in this community. Over one hundred species of forbs have been collected in the big sagebrush community, conspicuous and abundant among which are various species of *Antennaria, Arenaria congesta, Aster* spp., *Balsamorrhiza sagittata,* several species of *Erigeron, Eriogonum subalpinum, Geranium nervosum, Gilia aggregata, Lomatium* spp., *Potentilla* spp., *Senecio* spp., *Taraxacum officinale,* and *Viguiera multiflora.*

## THE LODGEPOLE PINE COMMUNITY

Lodgepole pine stands occur on well drained sandy soils on the higher terraces in the Jackson Hole Wildlife Park. They also constitute the typical coniferous community of the floor of Jackson Hole, where they occur conspicuously on the moraines which rise a few feet above the extensive sagebrush-covered outwash plains.

Throughout late summer and early fall the sites occupied by lodgepole pine are normally very dry. The soil is porous and its surface is well above the water table. For a prolonged period during the beginning of the growing season the soil remains moist as a result of the slow melting of the snow beneath the dense pine canopy. Early summer warmth provides a flourishing ground cover which gradually wanes in conspicuousness as the drier conditions of midsummer and fall come on.

Outstanding subordinate species within the lodgepole pine stands include: the red-fruited whortleberry (*Vaccinium scoparium*), a low shrub with conspicuous green stems; bluejoint (*Calamagrostis canadensis*), whose verdant appearance gives a semi-meadowlike look to the floor of this forest during much of the growing season; and heart-leaf arnica (*Arnica cordifolia*), with its large flowers and carpet of characteristic leaves.

Throughout this portion of the Rocky Mountain region, lodgepole pine communities are normally subclimax, and they are eventually followed in succession by the climax forest whose dominants are Engelmann spruce (*Picea engelmanni*) and alpine fir (*Abies lasiocarpa*). Lodgepole pine stands usually owe their origin to fire. Because of the relatively arid and cold microclimate, the relatively poor soil, and the short growing season for the region

as a whole, the rate at which the pine stand develops and the rate at which it is succeeded by spruce and fir are both very slow. It normally takes about two hundred years for the lodgepole pine community to mature and for any appreciable amount of spruce or fir reproduction to appear within it.

All of the areas where lodgepole pine now occurs within the Park were apparently burned over about seventy years ago. The stands are essentially even-aged and are about sixty years old. Charred detritus may be found not only on the surface of the ground, but also deep within the soil profile. Only an occasional fir seedling or sapling is present to indicate the trend of the succession.

Eighty-two species of vascular plants have been collected within the lodgepole pine stands of the Park. These include two tree species, ten species of shrubs, sixteen of grasses, and fifty-four of forbs.

## The Spruce-Fir Community

The steep north slope of Signal Mountain is covered by the true climax forest of the region. Engelmann spruce and alpine fir are the dominants. This community extends into that small portion of the Jackson Hole Wildlife Park which lies on the south side of the Snake River.

The site is both cool and moist. Snow lies within the forest late in the season, and as it melts it provides an abundance of soil moisture which lasts well into midsummer. In addition, the supply of soil moisture is continuously augmented by springs.

The soil of the spruce-fir forest is derived from till which was piled high on the base of the mountain by the glaciers. A podsol-like profile may be found, although the horizons are not perfectly differentiated and the leached horizon is only spasmodically encountered. The humus is of the mor type.

Mosses and lichens flourish. The shrubs are vigorous and abundant. There is good evidence of the dominant arborescent species being able to reproduce on the area, since all size classes of both spruce and fir occur. On a certain few places where landslides or avalanches have removed the soil mantle, successional vegetation may be found.

Besides the climax dominants, other tree species include lodgepole pine, Douglas fir, and limber pine (*Pinus flexilis*), all of which occur locally within this forest community, most often where there has been some minor disturbance. Fourteen species of shrubs have been collected, perhaps the most conspicuous of which are rusty menziesia (*Menziesia ferruginea*), mountain lover (*Pachystima myrsinites*), Utah honeysuckle (*Lonicera utahensis*), and big whortleberry (*Vaccinium membranaceum*). The twinflower (*Linnaea borealis*) is abundant. Grasses occur infrequently within this community and are represented by less than ten species and very few individuals. Outstanding among the thirty or more species of forbs are *Antennaria racemosa, Arnica cordifolia* and *A. subplumosa, Geranium richardsonii* and *G. viscosissimum, Osmorhiza chilensis, Pyrola* spp., *Saxifraga punctata,* and *Streptopus amplexifolius.*

### THE PLANTS OF WASTE PLACES

Bridle paths, abandoned roadways, roadside margins, gravel pits, an old ranch yard, and excessively trodden and burned picnic spots constitute the waste areas within the Jackson Hole Wildlife Park. The plants which occur on such sites hardly form recognizable communities. Many of the weeds of the region, a few species remaining from previous cultivation, and a variety of native species normally occur on such areas. The pea tree (*Caragana arborescens*) and the cultivated currant (*Ribes sativum*) have both survived abandonment and flourish amid a tangle of weeds. Especially noteworthy grasses of the waste sites include *Agrostis hiemalis, Bromus commutatus, B. japonicus, Elymus condensatus, Hordeum jubatum, Phleum pratense,* and *Sitanion hystrix.* Most important among the forbs are: (1) members of the composite family, including *Cirsium arvense, Conyza canadensis, Grindelia squarrosa, Iva xanthifolia, Lactuca integrata, Madia glomerata, Matricaria suaveolens, Taraxacum officinale,* and *Tragopogon porrifolius;* (2) members of the mustard family, including *Arabis exilis, Capsella bursa-pastoris, Descurainia* spp., *Lepidium campestre, L. perfoliatum,* and *Thlaspi arvense;* and (3) the following borages, *Cryptantha affinis, Hackelia floribunda, Lappula cenchroides,* and *L. foliosa.*

## The Flora

Four hundred and forty-nine species of vascular plants have been collected in the Jackson Hole Wildlife Park and its immediate vicinity. Five of these are fern allies, the remainder spermatophytes. Two hundred and twenty-four genera in 64 families are represented.

Composites are represented by 32 genera and 72 species. Twenty-four genera and 54 species of grasses were collected. Other groups abundantly represented are the sedges, legumes, and Rosaceae, each with 22 species: the Cruciferae, with 20 species; the Scrophulariaceae, with 19 species; the Ranunculaceae, with 16 species; and the Salicaceae, with 13 species. Thirty-three of the 64 families are represented by a single genus; 21 are represented by a single species.

Outstandingly large genera include *Carex,* which has 17 species in the area, and *Salix* which has 10 species and several varieties.

Nine arborescent species are indigenous to the immediate area. Six of these are conifers, and the remaining three are all members of the genus *Populus.* Forty-nine species of shrubs have been found, of which only two species are exotic.

The following list of the vascular plants is annotated to show the relative abundance of each species in the various plant communities that have been recognized. The usual abundance scale has been used in which the progression is from rare through occasional, common, and abundant to very abundant. The arrangement of families follows the usual phylogenetic scheme of standard manuals. Genera are arranged alphabetically within families, as are species within genera, and varieties within species.

## LIST OF VASCULAR PLANTS

### EQUISETACEAE

*Equisetum arvense* L.—Abundant on mud, wet sand, in the meadows, shrub-swamp, moist aspen groves, and spruce-fir forest.

*Equisetum arvense* L. var. *alpestre* Wahl.—Abundant on mud and wet sand.

*Equisetum hiemale* L.—Occasional in the streamside forest.

*Equisetum laevigatum* A. Br.—Abundant in the sedge meadow and streamside forest. Very abundant in the silver sagebrush community and along streambeds.

*Equisetum variegatum* Schleich.—Common along streambeds, in the streamside forest, and in the big sagebrush community.

### SELAGINELLACEAE

*Selaginella densa* Rydb.—Abundant with big sagebrush.

### PINACEAE

*Abies lasiocarpa* (Hook.) Nutt.—Occasional with lodgepole pine. Abundant in the spruce-fir forest.

*Juniperus communis* L.—Abundant under lodgepole pine.

*Picea engelmanni* Parry ex Engelm.—Very abundant in the spruce-fir forest.

*Picea pungens* Engelm.—Abundant in the streamside forest.

*Pinus contorta* Dougl.—Occasional in the streamside forest and big sagebrush community. Common in the spruce-fir forest. Very abundant in the lodgepole pine community.

*Pinus flexilis* James.—Occasional in the spruce-fir forest.

*Pseudotsuga taxifolia* (Poir.) Britt.—Rare in the hillside aspen ocmmunity. Common in the spruce-fir forest.

### TYPHACEAE

*Typha latifolia* L.—Locally abundant in wet areas.

### SPARGANIACEAE

*Sparganium androcladum* (Engelm.) Morong.—Very abundant in ponds and sluggish streams.

*Sparganium angustifolium* Michx.—Rare in beaver ponds.

### NAJADACEAE

*Potamogeton filiformis* Pers.—Abundant in ponds.

*Potamogeton lucens L.*—Abundant in ponds and streams.

*Potamogeton perfoliatus* L.—Occasional in running water.

*Potamogeton pusillus* L.—Common in ponds and streams.

*Potamogeton richardsonii* (Benn.) Rydb.—Abundant in ponds and sluggish streams.

*Potamogeton tenuifolius* Raf.—Common in ponds and streams.

### ALISMACEAE

*Sagittaria arifolia* (Nutt.) J. G. Smith.—Abundant in pools.

### GRAMINEAE

*Agropyron albicans* Scribn & Smith.—Occasional in the big sagebrush community.

*Agropyron dasystachyum* (Hook.) Scribn.—Occasional in the big sagebrush community.

*Agropyron subsecundum* (Link.) Hitchc.—Occasional in the streamside forest, intervale, and in the silver sagebrush community. Common under aspen, in the big sagebrush community, and in waste places.

*Agropyron trachycaulum* (Link.) Steud.—Common in the sedge-grass meadow, streamside forest, intervale, under aspen, in both sagebrush communities, under lodgepole pine, and in waste places.

*Agropyron trachycaulum* (Link.) Steud.var. *novae-angliae* Fern.—Occasional in the streamside forest. Common in moist aspen groves.

*Agrostis alba* L.—Abundant along streambeds and in the intervale. Common in the streamside forest and in moist aspen groves.

*Agrostis exarata* Trin.—Abundant in lodgepole pine forest. Occasional in waste places and in the streamside forest.

*Agrostis hiemalis* (Walt.) B. S. P.—Very abundant in the intervale and in waste places. Common along streambeds, in the streamside forest, the sedge-grass meadow, moist aspen groves, the lodgepole pine forest, and big sagebrush community.

*Alopecurus aequalis* Sobol.—Common on mud and on wet sandy areas in streambeds. Occasional in the sedge meadow.

*Beckmannia syzigachne* (Steud.) Fern.—Occasional in the sedgegrass meadow. Rare along streambeds.

*Bromus anomalus* Rupr.—Abundant in the silver sagebrush and lodgepole pine communities. Occasional in the big sagebrush and spruce-fir communities and in waste places.

*Bromus carinatus* H. & A.—Abundant under aspen. Occasional in the streamside forest and in both sagebrush communities.

*Bromus ciliatus* L.—Abundant in the shrub-swamp and in the streamside forest. Occasional in both sagebrush communities, moist aspen groves, and the spruce-fir forest.

*Bromus commutatus* Schrad.—Occasional along roadsides.

*Bromus inermis* Leyss.—Very abundant in the intervale. Occasional in the sedge-grass meadow, moist aspen groves, and waste places.

*Bromus japonicus* Thunb.—Occasional along roadsides.

*Bromus tectorum* L.—Common along streambeds, in waste places, and in the big sagebrush community.

*Calamagrostis canadensis* (Michx.) Beauv.—Abundant in the shrub-swamp, streamside forest, lodgepole pine and spruce-fir forests. Common in the intervale and moist aspen groves. Occasional in the hillside aspen community.

*Calamagrostis inexpansa* A. Gray.—Common under lodgepole pine. Occasional in the shrub-swamp.

*Dactylis glomerata* L.—Occasional under lodgepole pine.

*Danthonia intermedia* Vasey.—Common in the sedge-grass meadow, streamside forest, both sagebrush communities, and the coniferous forests.

*Deschampsia caespitosa* (L.) Beauv.—Common in the sedge-grass meadow, intervale, streamside forest, and moist aspen glades. Occasional in streambeds.

*Elymus condensatus* Presl.—Abundant in waste places.

*Festuca idahoensis* Elmer.—Abundant in both sagebrush communities. Common in the hillside aspen and streamside forests. Occasional in the sedge-grass meadows and moist aspen groves.

*Glyceria borealis* (Nash) Batch.—Common at the margin of open water.

*Glyceria elata* (Nash) Hitchc.—Common at the margin of open water, on wet sod, and in the shrub-swamp.

*Glyceria pauciflora* Presl.—Common along streambeds and in the streamside forest.

*Glyceria striata* (Lam.) Hitchc.—Common along streambeds.

*Hierochloe odorata* (L.) Beauv.—Occasional in the streamside forest.

*Hordeum brachyantherum* Nevski.—Common along streambeds and in the sedge-grass meadow. Occasional in the intervale, streamside forest, and silver sagebrush community.

*Hordeum jubatum* L.—Abundant in waste places. Occasional along streambeds and in the sedge-grass meadow.

*Koeleria cristata* (L.) Pers.—Abundant in both sagebrush communities. Common in the streamside forest. Occasional in the intervale.

*Melica spectabilis* Scribn.—Abundant under aspen and in the silver sagebrush community. Common in the sedge-grass meadow, shrub-swamp, and the big sagebrush community.

*Muhlenbergia andina* (Nutt.) Hitchc.—Abundant on wet sand in streambeds.

*Muhlenbergia filiformis* (Thurb.) Rydb.—Common on ant hills in the sedge-grass meadow. Occasional on sand in streambeds.

*Muhlenbergia racemosa* (Michx.) B. S. P.—Common in the streamside forest.

*Muhlenbergia richardsonis* Rydb.—Abundant in the streamside forest. Common in the sedge-grass meadow and in the silver sagebrush community.

*Phalaris arundinacea* L.—Occasional on wet sod.

*Phleum pratense* L.—Very abundant in the intervale. Abundant in the sedge-grass

meadow and in waste places. Common in the shrub-swamp, along streambeds, in the streamside forest, in both sagebrush communities, and under lodgepole pine.

*Poa annua* L.—Common on wet sod. Occasional in the big sagebrush community.

*Poa canbyi* (Scribn.) Piper.—Abundant in moist aspen groves and in the big sagebrush community. Common in the intervale, in the silver sagebrush community, and under aspen on hillsides.

*Poa fendleriana* (Steud.) Vasey.—Abundant in the big sagebrush community. Common in the intervale.

*Poa interior* Rydb.—Common in the big sagebrush community. Occasional in the silver sagebrush community.

*Poa leptocoma* Trin.—Common in the shrub-swamp.

*Poa nervosa* (Hook.) Vasey.—Abundant under hillside aspen and in the lodgepole pine forest.

*Poa palustris* L.—Common in the sedge-grass meadow and along streambeds. Occasional in big sagebrush stands.

*Poa pratensis* L.—Abundant in both sagebrush communities, the intervale, and the streamside forest. Common in the shrub-swamp, moist aspen groves, and the lodgepole pine forest.

*Sitanion hystrix* (Nutt.) J. G. Smith.—Common in waste places. Occasional in the hillside aspen and big sagebrush communities.

*Sphenopholis obtusata* (Michx.) Scribn.—Occasional in streambeds.

*Stipa columbiana* Macoun.—Abundant in the silver sagebrush community. Common in the streamside forest, intervale, and the lodgepole pine forest. Occasional in the big sagebrush community.

*Stipa comata* Trin. & Rupr.—Abundant in the big sagebrush and hillside aspen communities.

*Stipa lettermanni* Vasey.—Abundant in the big sagebrush and hillside aspen communities. Common in the silver sagebrush community and the intervale.

*Stipa richardsoni* Link.—Common in the streamside forest and lodgepole pine community.

*Trisetum spicatum* (L.) Richt.—Abundant in the coniferous forest communities.

*Trisetum wolfii* Vasey.—Occasional in the silver sagebrush community.

## Cyperaceae

*Carex aquatilis* Wahl.—Abundant at the margins of open water. Common in the sedge meadow.

*Carex arthrostachya* Olney.—Common on mud and in the sedge meadow.

*Carex aurea* Nutt.—Common on wet sod.

*Carex chimaphila* Holm.—Common along streambeds.

*Carex douglasii* Boott.—Abundant in waste places. Common at the margin of the streamside forest.

*Carex eastwoodiana* Stacey.—Abundant in the sedge-grass meadow, intervale, and silver sagebrush community. Common in the big sagebrush community.

*Carex festivella* Mack.—Common along streambeds, in the shrub-swamp, and in moist aspen groves.

*Carex geyeri* Boott.—Abundant in the coniferous forests. Occasional in hillside aspen stands.

*Carex gravida* Bailey.—Abundant in the intervale and silver sagebrush communities.

*Carex hoodii* Boott.—Common in the sedge-grass meadow, moist aspen groves, and the silver sagebrush communities.

*Carex interior* Bailey.—Common in the sedge-grass meadow. Occasional in the big sagebrush and lodgepole pine communities.

*Carex lanuginosa* Michx.—Common on wet sod, the sedge and sedge-grass meadows. Occasional in the intervale.

*Carex nebraskensis* Dewey.—Abundant at the margins of open water, on wet sod, and in the sedge meadow.

*Carex occidentalis* Bailey.—Common on wet sod and in the sedge meadow.

*Carex phaeocephala* Piper.—Common in the sedge-grass meadow.

*Carex rostrata* Stokes.—Abundant at the margins of open water.

*Carex vesicaria* L.—Common at the margins of open water.

*Eleocharis acicularis* (L.) R. & S.—Very abundant on mud.

*Eleocharis macrostachya* Britt.—Abundant on mud. Common in very shallow water, on wet sod, and in both the sedge and sedge-grass meadows.

*Eleocharis obtusa* (Willd.) Schultes.—Common in the sedge and sedge-grass meadows.

*Eleocharis pauciflora* (Lightf.) Link.—Common on wet sand in streambeds and in the sedge-grass meadow.

*Scirpus subterminalis* Torr.—Rare in beaver ponds.

### LEMNACEAE

*Lemna minor* L.—Abundant on the surface of quiet water.

*Lemna trisulca* L.—Occasional on the surface of quiet water.

### JUNCACEAE

*Juncus balticus* Willd.—Common on wet sod. Occasional in the silver sagebrush community.

*Juncus bufonius* L.—Abundant on moist sand in streambeds.

*Juncus confusus* Coville.—Common in the sedge-grass meadow, intervale, and in both sagebrush communities.

*Juncus ensifolius* Wikst.—Abundant on mud and in wet sand in streambeds. Common in the sedge and sedge-grass meadows.

*Juncus filiformis* L.—Rare in the sedge-grass meadow.

*Juncus longistylis* Torr.—Abundant on mud and in wet sand in streambeds. Common in the sedge meadow.

*Juncus parryi* Engelm.—Abundant along streambeds. Common in the sedge-grass meadow and in the streamside forest.

*Juncus saximontanus* A. Nels.—Common along streambeds.

### LILIACEAE

*Allium brevistylum* Wats.—Common in the streamside forest, moist aspen groves, and in the spruce-fir forest.

*Brodiaea douglasii* Wats.—Rare in the shrub-swamp.

*Camassia quamash* (Pursh) Greene.—Occasional in moist aspen groves.

*Fritillaria atropurpurea* Nutt.—Common in the big sagebrush community.

*Fritillaria pudica* (Pursh) Spreng.—Abundant in the big sagebrush community.

*Smilacina stellata* (L.) Desf.—Abundant in the shrub-swamp, streamside forest, and moist aspen glades. Common under lodgepole pine.

*Streptopus amplexifolius* (L.) DC.—Common in the spruce-fir forest.

*Zygadenus paniculatus* (Nutt.) Wats.—Common in the big sagebrush community.

### IRIDACEAE

*Sisyrinchium idahoense* Bickn.—Occasional in moist sod along the streambeds.

### ORCHIDACEAE

*Calypso bulbosa* (L.) Oakes.—Abundant in the streamside forest. Common in the coniferous forests.

*Corallorhiza mertensiana* Bong.—Occasional in the lodgepole pine forest.

*Corallorhiza striata* Lindl.—Occasional in the lodgepole pine forest.

*Habenaria hyperborea* (L.) R. Br.—Occasional in the sedge-grass meadow, the shrub-swamp, and under willows in the streambeds.

*Spiranthes romanzoffiana* Cham.—Abundant in the sedge-grass meadows. Occasional in the intervale.

### SALICACEAE

*Populus angustifolia* James.—Abundant in the streamside forest. Common on the higher portions of the streambeds.

*Populus balsamifera* L.—Common in the streamside forest. Occasional on the higher portions of the streambed.

*Populus tremuloides* Michx.—Very abundant in stands on hillsides and in moister habitats on the level. Occasional in the big sagebrush community and the streamside

forest.

*Salix caudata* (Nutt.) Heller.—Common in streambeds. Occasional in the shrub-swamp and the streamside forest.

*Salix caudata* (Nutt.) Heller var. *bryantiana* Ball & Bracelin.—Common in streambeds, the shrub-swamp, and streamside forest.

*Salix caudata* (Nutt.) Heller var. *parvifolia* Ball.—Occasional in the shrub-swamp and streamside forest.

*Salix commutata* Bebb.—Rare in the shrub-swamp.

*Salix drummondiana* Barr. var. *subcoerulea* (Piper) Ball ined.—Very abundant in the shrub-swamp. Abundant along streambeds and in the streamside forest.

*Salix geyeriana* Anders.—Very abundant in the shrub-swamp. Abundant in the streamside forest. Common along streambeds.

*Salix lutea* Nutt.—Occasional in the streamside forest.

*Salix lutea* Nutt. var. *platyphylla* Ball.—Occasional along streambeds and in the streamside forest.

*Salix mackenziana* (Hook.) Barr.—Occasional along streambeds and in the streamside forest.

*Salix melanopsis* Nutt.—Occasional along streambeds.

*Salix melanopsis* Nutt. var. *tenerrima* (Hend.) Ball.—Very abundant along streambeds and in the streamside forest.

*Salix pseudocordata* (Anders.) Rydb. var. *aequalis* Anders.—Very abundant in the shrub-swamp. Abundant in the streamside forest. Common in moist aspen glades.

*Salix scouleriana* Barr.—Common in the spruce-fir forest. Rare in the lodgepole pine community.

*Salix wolfii* Bebb.—Very abundant in the shrub-swamp. Common in the streamside forest.

*Salix wolfii* Bebb var. *idahoensis* Ball.—Occasional in the shrub-swamp.

### BETULACEAE

*Alnus tenuifolia* Nutt.—Abundant on higher portions of the streambeds. Common in the shrub-swamp and the streamside forest.

*Betula glandulosa* Michx.—Common in the shrub-swamp. Occasional in the streamside forest.

### CANNABINACEAE

*Humulus lupulus* L.—Common in waste places.

### URTICACEAE

*Urtica gracilis* Ait.—Abundant along roadsides and in other waste places.

### SANTALACEAE

*Comandra pallida* A. DC.—Abundant in the big sagebrush community.

### LORANTHACEAE

*Arceuthobium americanum* Nutt.—Abundant and parasitic on lodgepole pine.

### POLYGONACEAE

*Eriogonum subalpinum* Greene.—Very abundant in the big sagebrush community. Abundant in the silver sagebrush community and in the intervale. Common in the streamside forest.

*Eriogonum umbellatum* Torr.—Occasional in streambeds.

*Polygonum amphibium* L.—Abundant in ponds and pools. Common on mud.

*Polygonum aviculare* L.—Abundant on sod and in waste places.

*Polygonum bistortoides* Pursh.—Very abundant in the sedge-grass meadow and intervale. Abundant in the silver sagebrush community.

*Polygonum buxiforme* Small.—Abundant in waste places.

*Polygonum douglasii* Greene.—Very abundant in hillside aspen, intervale, and both sagebrush communities. Abundant in the streamside forest and the sedge-grass meadow. Common in moist aspen groves and in the lodgepole pine forests.

*Polygonum fluitans* Eaton.—Occasional at the margins of ponds and on adjacent muddy shores.

*Rumex acetosella* L.—Abundant in waste places.

*Rumex crispus* L.—Common in the shrub-swamp, intervale, and on waste places.

*Rumex fueginus* Phillipi.—Occasional on mud and adjacent wet sod.

*Rumex paucifolius* Nutt.—Abundant in the streamside forest, intervale, and both sagebrush communities.

*Rumex triangulivalvis* (Danser) Rech.—Occasional in gravelly streambeds.

CHENOPODIACEAE

*Blitum capitatum* L.—Common in sandy streambeds and waste places. Occasional in lodgepole pine forests.

*Chenopodium album* L.—Common in sandy streambeds and waste places.

*Chenopodium aridum* A. Nels.—Common in sandy streambeds, roadsides, and other waste places.

*Kochia scoparia* Schrad.—Common in waste places.

*Monolepis nuttalliana* (R. & S.) Engelm.—Common in waste places. Occasional in lodgepole pine forests.

*Salsola pestifer* A. Nels.—Common in waste places.

PORTULACACEAE

*Claytonia lanceolata* Pursh.—Abundant in the big sagebrush and lodgepole pine communities. Common in the sedge-grass meadow.

*Lewisia minima* A. Nels.—Rare in the big sagebrush community.

CARYOPHYLLACEAE

*Arenaria congesta* Nutt.—Very abundant in the big sagebrush community. Abundant in the streamside forest and the intervale. Common in the silver sagebrush and lodgepole pine communities.

*Arenaria lateriflora* L.—Occasional in moist aspen groves.

*Cerastium oreophilum* Greene.—Abundant in the shrub-swamp, intervale, and both sagebrush communities. Common under lodgepole pine.

*Sagina saginoides* (L.) Britt.—Abundant in well-trodden waste places. Common along streambeds.

*Spergularia rubra* (L.) Presl.—Abundant in waste places. Common in the shrub-swamp, sedge-grass meadow, and big sagebrush community.

*Stellaria longifolia* Muhl.—Common in the shrub-swamp. Occasional on mud and in the lodgepole pine forest.

*Stellaria longipes* Goldie.—Abundant in the sedge-grass meadow.

NYMPHAECEAE

*Nuphar polysepalum* Engelm.—Abundant in many ponds.

RANUNCULACEAE

*Aconitum columbianum* Nutt.—Abundant in moist aspen groves. Common in the sedge-grass meadow, shrub-swamp, and streamside forest.

*Actaea rubra* (Ait.) Willd.—Common in the spruce-fir forest. Occasional in the shrub-swamp.

*Anemone globosa* Nutt.—Occasional in the streamside forest.

*Clematis columbiana* T. & G.—Common in the streamside forest.

*Clematis eriophora* Rydb.—Common in moist aspen glades. Occasional in both sagebrush communities.

*Delphinium nelsoni* Greene.—Very abundant in the big sagebrush community and the intervale. Abundant in the sedge-grass meadow, hillside aspen, and silver sagebrush community. Common in the shrub-swamp, streamside forest, and streambeds.

*Delphinium occidentale* (Wats.) Wats.—Abundant in the shrub-swamp, moist aspen groves, and both sagebrush communities. Common in the intervale. Occasional in the streamside forest.

*Ranunuclus acriformis* A. Gray var. *montanensis* (Rydb.) Bens.—Abundant in the intervale. Common in the shrub-swamp.

*Ranunculus aquatilis* L. var. *capillaceus* (Thuill.) DC.—Abundant in pools, sluggish streams, and ponds.

*Ranunculus cymbalaria* (Pursh) Greene.—Abundant on wet sand in streambeds. Common on mud.

*Ranunculus glaberrimus* Hook.—Common under lodgepole pine.

*Ranunculus inamoenus* Greene.—Abundant in the intervale. Occasional in sedge meadow and shrub-swamp.

*Ranunculus natans* C. A. Meyer.—Abundant in ponds and pools. Common on mud.

*Ranunculus sceleratus* L. var. *multifidus* Nutt.—Abundant in shallow water and on adjacent muddy shores.

*Thalictrum fendleri* Engelm.—Abundant in moist aspen groves. Occasional in the silver sagebrush community.

*Thalictrum occidentale* Gray.—Common in the shrub-swamp, moist aspen groves, and spruce-fir community. Rare in the intervale.

### BERBERIDACEAE

*Mahonia aquifolium* (Pursh) Nutt.—Abundant under aspen and lodgepole pine. Common in the spruce-fir community. Occasional in the big sagebrush community.

### CRUCIFERAE

*Arabis drummondiii* A. Gray.—Abundant in the intervale and big sagebrush community.

*Arabis exilis* A. Nels.—Abundant in waste places.

*Arabis glabra* (L.) Bernh.—Common in the silver sagebrush community.

*Arabis hirsuta* Scop.—Common in the intervale.

*Arabis holboellii* Hornem.—Very abundant in the intervale. Abundant in the streamside forest and in both sagebrush communities.

*Arabis nuttallii* Robinson.—Common in the intervale.

*Barbarea americana* Rydb.—Occasional on mud.

*Capsella bursa-pastoris* (L.) Medic.—Abundant in waste places. Common in the intervale and in lodgepole pine forests.

*Cardamine breweri* Wats.—Common on mud. Occasional in the spruce-fir forest.

*Descurainia pinnata* (Walt.) Britt.—Common in the big sagebrush community and in waste places.

*Descurainia sophia* (L.) Webb.—Common in waste places.

*Draba stenoloba* Ledeb. var. *nana* (Schulz) Hitchc.—Abundant in the sedge-grass meadow, intervale, moist aspen glades, and in both sagebrush communities.

*Erysimum cheiranthoides* L.—Occasional in moist aspen groves.

*Lepidium campestre* (L.) R. Br.—Abundant in waste places.

*Lepidium densiflorum* Schrad. var. *bourgeauanum* (Thell.) Hitchc.—Abundant in the big sagebrush community.

*Lepidium perfoliatum* L.—Common on steep banks along streambeds and in other waste places.

*Lesquerella prostrata* A. Nels.—Rare on sandy areas in streambeds.

*Rorippa palustris* (L.) Bess.—Abundant in shallow pools and in wet areas along streambeds.

*Thlaspi arvense* L.—Abundant in waste places. Common in intervale and in the big sagebrush community.

*Thlaspi parviflorum* A. Nels.—Abundant in the intervale.

### CRASSULACEAE

*Sedum stenopetalum* Pursh.—Abundant in the big sagebrush community.

### SAXIFRAGACEAE

*Lithophragma bulbifera* Rydb.—Abundant in the sedge-grass meadow, intervale, hillside aspen, and both sagebrush communities.

*Lithophragma parviflora* Nutt.—Abundant in the streamside forest. Common in hillside aspen stands.

*Parnassia parviflora* DC.—Common in the sedge meadow and on moist areas along the streambeds.

*Saxifraga montanensis* Small.—Abundant in the silver sagebrush community.

*Saxifraga punctata* L. var. *arguta* (D. Don) Engelm. & Irmsch.—Common in the spruce-fir forest.

GROSSULARIACEAE

*Ribes inerme* Rydb.—Abundant in the shrub-swamp. Common in the streamside forest, moist aspen groves, and moist waste places.

*Ribes lacustre* (Pers.) Poir.—Common in the spruce-fir forest, and under lodgepole pine.

*Ribes sativum* Syme.—Remaining from previous cultivation in an abandoned ranch yard.

*Ribes setosum* Lindl.—Common in the streamside forest and moist aspen groves

*Ribes viscosissimum* Pursh.—Abundant in the spruce-fir forest.

ROSACEAE

*Amelanchier alnifolia* Nutt.—Abundant under aspen on hillsides. Common along drier portions of streambeds, in moist aspen groves, and in the big sagebrush and lodgepole pine communities.

*Fragaria bracteata* Heller.—Common in the big sagebrush community.

*Fragaria glauca* (S. Wats.) Rydb.—Abundant in the streamside forest. Common under aspen and in the big sagebrush community.

*Fragaria pauciflora* Rydb.—Common under lodgepole pine.

*Fragaria platypetala* Rydb.—Common in the silver sagebrush community. Occasional under lodgepole pine.

*Geum macrophyllum* Willd.—Abundant in the shrub-swamp. Common in the streamside forest and in waste places.

*Potentilla arguta* Pursh ssp. *convallaria* (Rydb.) Keck.—Abundant in the lodgepole pine forest. Common under spruce and fir.

*Potentilla arguta* Pursh ssp. *typica* Keck.—Abundant in the intervale and in both sagebrush communities.

*Potentilla diversifolia* Lehm.—Abundant in the sedge-grass meadow and the intervale.

*Potentilla flabelliformis* Lehm.—Abundant in the silver sagebrush community. Common in the intervale, moist aspen groves, the big sagebrush community, and the coniferous forests.

*Potentilla fruticosa* L.—Common in the shrub-swamp and in the silver sagebrush community. Occasional in the streamside forest and in moist aspen groves.

*Potentilla gracilis* Dougl. ssp. *nuttallii* (Lehm.) Keck.—Abundant in moist aspen groves. Common in the shrub-swamp, streamside forest, intervale, and in the big sagebrush and lodgepole pine communities.

*Potentilla monspeliensis* L.—Occasional along streambeds.

*Potentilla pulcherrima* Lehm.—Common in the intervale and lodgepole pine forests.

*Prunus melanocarpa* (A. Nels.) Rydb.—Abundant under aspen on hillsides. Common along streambeds and in waste places.

*Purshia tridentata* DC.—Localliy abundant in the big sagebrush community.

*Rosa fendleri* Crepin.—Common in the spruce-fir forest.

*Rosa woodsii* Lindl.—Abundant in the streamside forest. Common in the hillside aspen and lodgepole pine stands.

*Rubus parviflorus* Nutt.—Common along streambeds and in the spruce-fir forest.

*Rubus strigosus* Michx.—Occasional along the drier portions of the streambeds.

*Sieversia ciliata* G. Don.—Abundant in both sagebrush communities.

*Sorbus scopulina* Greene.—Common in the spruce-fir forest. Occasional under lodgepole pine.

*Spiraea lucida* Dougl.—Abundant in the spruce-fir forest. Common under lodgepole pine.

LEGUMINOSAE

*Astragalus agrestis* Dougl.—Common in the sedge-grass meadow.

*Astragalus alpinus* L.—Abundant in the streamside forest. Common in the shrub-swamp.

*Astragalus bodini* Sheld.—Occasional in the streamside forest.

*Astragalus decumbens* (Nutt.) Gray var. *oblongifolius* (Rydb.) Cronq.—Common in lodgepole pine stands.

*Astragalus glareosus* Dougl.—Common in the streamside forest.

*Caragana arborescens* Lam.—Remaining from cultivation in an abandoned ranch yard.

*Glycyrrhiza lepidota* Pursh.—Abundant in waste places.

*Hedysarum boreale* Nutt. var. *cinerascens* (Rydb.) Rollins.—Abundant locally in the big sagebrush community.

*Lupinus argenteus* Pursh.—Common in the big sagebrush community.

*Lupinus humicola* A. Nels.—Abundant in the big sagebrush community.

*Lupinus lepidus* Dougl. ssp. *caespitosus* (Nutt.) Detling.—Abundant in drier sand along streambeds. Common in the intervale.

*Lupinus parviflorus* Nutt.—Abundant in the intervale, the silver sagebrush community, under hillside aspen, in moist aspen groves, and under lodgepole pine. Common in the spruce-fir forest.

*Medicago lupulina* L.—Common in the streamside forest, intervale, in the big sagebrush community, and in waste places.

*Medicago sativa* L.—Common in waste places.

*Melilotus alba* Desv.—Common in gravel along streambeds and in waste places.

*Melilotus officinalis* (L.) Lam.—Common in gravel along streambeds and in waste places.

*Oxytropis deflexa* (Pall.) DC.—Common in the streamside forest and the intervale. Occasional under willows in streambeds.

*Oxytropis deflexa* (Pall.) DC. var. *sericea* T. & G.—Common in the streamside forest.

*Trifolium hybridum* L.—Abundant in the intervale. Common in the sedge-grass meadow and in moist aspen groves.

*Trifolium pratense* L.—Abundant in the sedge-grass meadow. Common in waste places.

*Trifolium repens* L.—Common in some portions of big sagebrush communities.

*Trifolium rydbergii* Greene.—Abundant in the sedge-grass meadow, streamside forest, intervale, and both sagebrush communities. Common in moist aspen groves.

*Vicia americana* Muhl. var. *linearis* (Nutt.) Wats.—Common in the shrub-swamp.

LINACEAE

*Linum lewisii* Pursh.—Abundant in the big sagebrush and lodgepole pine communities. Common under aspen on hillsides and in the silver sagebrush community.

GERANIACEAE

*Geranium nervosum* Rydb.—Abundant in the shrub-swamp, under aspen on hillsides, and in the big sagebrush community. Common in the intervale.

*Geranium richardsonii* F. & M.—Abundant in moist aspen groves and in the spruce-fir forest.

*Geranium viscosissimum* F. & M.—Abundant in moist aspen groves and in the coniferous forests.

CALLITRICHACEAE

*Callitriche palustris* L.—Common in pools and adjacent mud.

LIMNANTHACEAE

*Floerkia occidentalis* Rydb.—Occasional in the intervale.

CELASTRACEAE

*Pachystima myrsinites* Raf.—Common in the spruce-fir forest.

ACERACEAE

*Acer glabrum* Torr.—Rare in the lodgepole pine community.

RHAMNACEAE

*Ceanothus velutinus* Dougl.—Occasional under aspen on hillsides.

*Rhamnus alnifolia* L'Her.—Common in dry waste places. Occasional in the shrub-swamp and under aspen.

MALVACEAE

*Sphaeralcea rivluaris* (Dougl.) Torr.—Common in the big sagebrush community and in waste places.

VIOLACEAE

*Viola adunca* Smith.—Abundant in the shrub-swamp, streamside forest, and intervale. Common in the sedge-grass meadow, moist aspen groves, and both sagebrush communities.

*Viola nephrophylla* Greene.—Common in the streamside forest.

ELAEAGNACEAE

*Elaeagnus commutata* Bernh.—Occasional along drier portions of streambeds and along the margins of the streamside forest.

*Shepherdia canadensis* (L.) Nutt.—Abundant in the streamside forest and in all coniferous forests.

ONAGRACEAE

*Epilobium adenocaulon* Hausskn.—Abundant on wet sod and in the shrub-swamp. Common on wet sand along streambeds.

*Epilobium angustifolium* L.—Abundant in the streamside forest, moist aspen groves, and the coniferous forests. Common in the hillside aspen and big sagebrush communities.

*Epilobium latifolium* L.—Abundant on coarse gravel strands in streambeds.

*Epilobium paniculatum* Nutt.—Common in the intervale and in the big sagebrush community.

*Epilobium saximontanum* Hausskn.—Common in the shrub-swamp and moist aspen groves.

*Epilobium suffruticosum* Nutt.—Common in gravel in streambeds.

*Gayophytum diffusum* T. & G.—Abundant in the big sagebrush community and in waste places.

*Oenothera heteranthera* Nutt.—Common in the sedge-grass meadow and the intervale. Occasional in the shrub-swamp.

HALORAGIDACEAE

*Hippuris vulgaris* L.—Occasional in pool, ponds, and sluggish streams.

*Myriophyllum verticillatum* L.—Common in beaver ponds.

UMBELLIFERAE

*Angelica pinnata* S. Wats.—Common in moist aspen groves.

*Heracleum lanatum* Michx.—Common locally in the shrub-swamp. Rare in moist aspen groves.

*Ligusticum filicinum* S. Wats.—Abundant in moist aspen groves. Occasional in the sedge-grass meadow.

*Lomatium ambiguum* (Nutt.) C. & R.—Abundant under aspen on hillsides and in the big sagebrush community.

*Lomatium dissectum* (Nutt.) Math. & Const. var. *multifidum* (Nutt.) Math. & Const.—Abundant in the big sagebrush community. Common in the shrub-swamp.

*Lomatium simplex* (Nutt.) Macbr.—Common in the lodgepole pine community. Occasional in the big sagebrush community.

*Osmorhiza chilensis* H. & A.—Abundant in the coniferous forests. Common in moist aspen groves.

*Osmorhiza obtusa* (C. & R.) Fern.—Common in all aspen stands.

*Osmorhiza occidentalis* (Nutt.) Torr.—Abundant in all aspen stands.

*Perideridia bolanderi* (A. Gray) Nels. & Macbr.—Common under aspen on hillsides

and in the big sagebrush community. Occasional in the silver sagebrush community and the intervale.

*Perideridia gairdneri* (H. & A.) Mathias.—Abundant in the intervale, streamside forest, hillside aspen, both sagebrush communities, and lodgepole pine stands. Common in moist aspen groves.

*Sium suave* Walt.—Occasional in shallow water in ponds.

### Cornaceae

*Cornus stolonifera* Michx.—Abundant on moist gravel along streambeds. Common in the spruce-fir forest.

### Ericaceae

*Arctostaphylos uva-ursi* (L.) Spreng.—Abundant in the lodgepole pine forest. Common in the streamside forest and in the spruce-fir community.

*Chimaphila umbellata* (L.) Nutt.—Occasional in the shrub-swamp and in the lodgepole pine forest.

*Menziesia ferruginea* Smith.—Abundant in the spruce-fir forest.

*Pterospora andromeda* Nutt.—Common in the lodgepole pine forest.

*Pyrola asarifolia* Michx.—Common in the spruce-fir forest. Occasional in the streamside forest.

*Pyrola chlorantha* Sw.—Abundant in the coniferous forests.

*Pyrola secunda* L.—Abundant in thte coniferous forests.

*Vaccinium membranaceum* Dougl.—Abundant in the spruce-fir forest. Occasional in the lodgepole pine stands.

*Vaccinium scoparium* Leiberg.—Very abundant in the lodgepole pine forests. Abundant under spruce-fir.

### Primulaceae

*Androsace septentrionalis* L. var. *puberulenta* (Rydb.) Knuth.—Abundant on wet sod, in the intervale, and in both sagebrush communities. Common under lodgepole pine.

*Androsace septentrionalis* L. var. *subumbellata* A. Nels.—Common in the streamside forest, hillside aspen, and the big sagebrush and lodgepole pine communities.

*Dodecatheon pauciflorum* (Durand) Greene.—Abundant in the sedge and sedge-grass meadows, the streamside forest, and the silver sagebrush community. Common in the intervale. Occasional in the big sagebrush community and in lodgepole pine stands.

### Gentianaceae

*Gentiana amarella* L.—Abundant in the streamside forest and in the lodgepole pine community.

*Gentiana forwoodii* Gray.—Abundant in the intervale. Common in the sedge-grass meadow, streamside forest, and silver sagebrush community.

*Gentiana thermalis* O. Ktze.—Abundant in the streamside forest. Common in the sedge and sedge-grass meadow. Occasional under willows in the streambeds.

*Swertia radiata* (Kellogg) Ktze.—Common in both sagebrush communities. Occasional under lodgepole pine.

### Polemoniaceae

*Collomia linearis* Nutt.—Abundant in the intervale, moist aspen groves, and both sagebrush communities.

*Gilia aggregata* (Pursh) Spreng.—Abundant in the big sagebrush community. Common in the intervale.

*Linanthus septentrionalis* Mason.—Occasional in the intervale.

*Phlox longifolia* Nutt. ssp. *calva* Wherry.—Abundant in the big sagebrush community.

*Phlox multiflora* A. Nels.—Common in the big sagebrush community.

*Polemonium caeruleum* L. var. *occidentalis* Greene.—Occasional in the sedge meadow.

*Polemonium pulcherrimum* Hook.—Abundant on sandy elevations near the streambeds.

### Hydrophyllaceae

*Hydrophyllum capitatum* Dougl.—Abundant in the shrub-swamp, under aspen on hillsides, and in the big sagebrush community. Common in the sedge-grass meadow.

*Nemophila breviflora* Gray.—Abundant under aspen and in the big sagebrush community. Common in the shrub-swamp and intervale.

*Phacelia franklinii* (R. Br.) Gray.—Common in the lodgepole pine stands.

*Phacelia heterophylla* Pursh.—Common in gravelly wastes.

*Phacelia leucophylla* Torr.—Common along streambeds and in the big sagebrush community.

BORAGINACEAE

*Cryptantha affinis* (Gray) Greene.—Common in waste places.

*Hackelia diffusa* (Lehm.) Jnstn. var. *caerulescens* (Rydb.) Jnstn.—Common in moist aspen groves and in the big sagebrush community.

*Hackelia floribunda* (Lehm.) Jnstn.—Abundant in waste places. Common in moist aspen groves.

*Lappula cenchroides* A. Nels.—Abundant in waste places. Common in the big sagebrush community.

*Lappula foliosa* A. Nels.—Common in waste places.

*Lithospermum ruderale* Dougl.—Abundant in the big sagebrush community. Common in the sedge-grass meadow and under aspen.

LABIATAE

*Agastache urticifolia* (Benth.) Ktze.—Abundant under aspen on hillsides. Common in moist aspen groves and in the big sagebrush commuunity.

*Dracocephalum parviflorum* Nutt.—Occasional in waste places.

*Mentha canadensis* L.—Abundant in the sedge meadow. Common on wet sod, in the shrub-swamp, along moist streambeds, and in the streamside forest.

*Prunella vulgaris* L.—Common in the streamside forest. Occasional in waste places.

*Scutellaria galericulata* L.—Abundant in the sedge meadow. Common in the shrub-swamp and on wet sod.

SCROPHULARIACEAE

*Castilleja flava* Wats.—Common in the big sagebrush community.

*Castilleja lineariaefolia* Benth.—Occasional under willows in streambeds and in the streamside forest.

*Castilleja longispica* A. Nels.—Common in the big sagebrush community.

*Castilleja lutea* Heller.—Common in the intervale.

*Castilleja miniata* Dougl.—Abundant in the shrub-swamp and spruce-fir forest. Common in the streamside forest.

*Castilleja rhexifolia* Rydb.—Abundant in the streamside forest. Common in the shrub-swamp.

*Collinsia parviflora* Lindl.—Very abundant in the streamside forest, intervale, and big sagebrush commnuity. Abundant under aspen and in lodgepole pine stands.

*Cordylanthus ramosus* Nutt.—Common in the big sagebrush community.

*Mimulus guttatus* DC.—Common in very shallow water, on mud, and in wet sand along streambeds.

*Orthocarpus luteus* Nutt.—Abundant in the streamside forest and intervale. Common in both sagebrush communities.

*Pedicularis groenlandica* Retz.—Abundant in the sedge meadow and the streamside forest.

*Pedicluaris paysoniana* Pennell.—Abundant in the coniferous forests. Common in moist aspen groves. Occasional in the silver sagebrush community.

*Pedicularis racemosa* Dougl.—Occasional in the spruce-fir forest.

*Penstemon deustus* Dougl.—Abundant in the big sagebrush community.

*Penstemon procerus* Dougl.—Abundant in the silver sagebrush community. Common in the sedge-grass meadow and intervale. Occasional under willows along streambeds and in the lodgepole pine forest.

*Penstemon subglaber* Rydb.—Abundant in the big sagebrush community.

*Veronica americana* Schwein.—Very abundant on mud. Abundant in the sedge meadow and on wet sand in streambeds.

*Veronica peregrina* L. var. *xalapensis* (H.B.K.) St. John & Warren.—Abundant on mud. Common in the sedge meadow.

*Veronica serpyllifolia* L. var. *humifusa* (Dicks.) Vahl.—Abundant on mud. Common in the sedge meadow.

### OROBANCHACEAE

*Orobanche fasciculata* Nutt.—Common in the big sagebrush community.
*Orobanche ludoviciana* Nutt.—Common in the big sagebrush community.
*Orobanche uniflora* L.—Abundant in the big sagebrush community.

### LENTIBULARIACEAE

*Utricularia vulgaris* L.—Rare in beaver ponds.

### PLANTAGINACEAE

*Plantago lanceolata* L.—Abundant in waste places.
*Plantago major* L.—Common in waste places.

### RUBIACEAE

*Galium bifolium* Wats.—Common under aspen on hillsides and in both sagebrush communities.

*Galium boreale* L.—Abundant in the streamside forest, moist aspen glades, and the coniferous forests. Common in the shrub-swamp, intervale, and silver sagebrush community.

*Galium trifidum* L.—Common in the shrub-swamp.

### CAPRIFOLIACEAE

*Linnaea borealis* L. var. *americana* (Forbes) Rehd.—Very abundant in the spruce-fir forest.

*Lonicera involucrata* Banks.—Very abundant in the streamside forest. Abundant in the shrub-swamp, moist aspen groves, and the coniferous forests.

*Lonicera utahensis* S. Wats.—Common under lodgepole pine.
*Sambucus melanocarpa* Gray.—Common in the spruce-fir forest.
*Symphoricarpos occidentalis* Hook.—Common in moist aspen groves.
*Symphoricarpos rivularis* Suks.—Abundant in waste places.
*Symphoricarpos tetonensis* A. Nels.—Abundant in lodgepole pine forests. Common in moist aspen groves and in big sagebrush community.

### VALERIANACEAE

*Valeriana obovata* (Nutt.) R. & S. ssp. *obovata* Meyer.—Abundant in the sedge-grass meadow. Common in moist aspen groves.

*Valeriana occidentalis* Heller.—Abundant in aspen stands. Common in the sedge-grass meadow and silver sagebrush community.

### CAMPANULACEAE

*Campanula rotundifolia* L.—Abundant in both sagebrush communities. Common in the streamside forest, intervale, and the coniferous forests.

### LOBELIACEAE

*Porterella carnosula* (H. & A.) Torr.—Occasional in shallow water at the margin of a pond and on the adjacent muddy shore.

### COMPOSITAE

*Achillea millefolium* L.—Very abundant in the intervale. Abundant in the streamside forest, both sagebrush communities, and the coniferous forests. Common in the sedge-grass meadow, along streambeds, under aspen, and in waste places.

*Agoseris elata* (Nutt.) Greene.—Common in the sedge-grass meadow.

*Agoseris glauca* (Nutt.) Greene.—Abundant in the sagebrush communities. Common in the sedge-grass meadow and under lodgepole pine.

*Agoseris glauca* (Nutt.) Greene var. *laciniata* (Eat.) Smiley.—Common in the intervale. Occasional in the sedge-grass meadow and the big sagebrush community.

*Agoseris purpurea* (A. Gray) Greene.—Abundant in the sedge-grass meadow. Common along streambeds, in the streamside forest, and under lodgepole pine.

*Antennaria aprica* Greene.—Common in the big sagebrush community.

*Antennaria arida* E. Nels.—Common in the big sagebrush community.

*Antennaria corymbosa* E. Nels.—Abundant in the intervale, both sagebrush communities, and the spruce-fir forest. Common in the sedge-grass meadow, moist aspen groves, and the lodgepole pine forest.

*Antennaria dimorpha* (Nutt.) T. & G.—Occasional in the big sagebrush community.

*Antennaria luzuloides* T. & G.—Common in the sedge-grass meadow and the intervale.

*Antennaria parvifolia* Nutt.—Abundant in the streamside forest. Common under willows in the streambeds.

*Antennaria racemosa* Hook.—Abundant in the spruce-fir forest.

*Antennaria rosea* (Eat.) Greene.—Abundant in the streamside forest, big sagebrush community, and under lodgepole pine.

*Arnica chamissonis* L.—Common in the shrub-swamp, along streambeds, and in moist aspen groves. Occasional in the big sagebrush community.

*Arnica cordifolia* Hook.—Very abundant in coniferous forests.

*Arnica latifolia* Bong.—Common in the coniferous forests.

*Artemisia abrotanum* L.—Remaining from previous cultivation.

*Artemisia cana* Pursh.—Very abundant in the silver sagebrush community. Occasional in the shrub-swamp, moist aspen groves, and the big sagebrush community.

*Artemisia dracunculoides* Pursh.—Occasional in waste places.

*Artemisia ludoviciana* Nutt. ssp. *candicans* (Rydb.) Keck.—Common along drier portions of streambeds.

*Artemisia ludoviciana* Nutt. ssp. *typica* Keck.—Common along drier portions of streambeds, in moist aspen glades, and on the intervale.

*Artemisia tridentata* Nutt.—Very abundant in the big sagebrush community. Occasional under aspen on hillsides.

*Artemisia tripartita* Rydb.—Common locally in the big sagebrush community.

*Aster campestris* Nutt.—Abundant in the intervale.

*Aster chilensis* Nees ssp. *adscendens* (Lindl.) Cronq.—Abundant in the streamside forest, sedge-grass meadow, intervale, both sagebrush communities, and the lodgepole pine forest. Occasional under willows in the streambeds.

*Aster coerulescens* DC. var. *laetevirens* (Greene) Cronq.—Abundant in the sedge-grass meadow. Common in the shrub-swamp, along streambeds, and in the streamside forest.

*Aster conspicuus* Lindl.—Abundant in the spruce-fir forest.

*Astre foliaceus* Lindl. var. *apricus* A. Gray.—Occasional in the lodgepole pine community.

*Aster foliaceus* Lindl. var. *frondeus* A. Gray.—Abundant in the streamside forest, moist aspen groves, and the coniferous forests. Common in the shrub-swamp and waste places.

*Aster integrifolius* Nutt.—Abundant under aspen. Common in the shrub-swamp and in both sagebrush communities. Occasional under lodgepole pine.

*Aster occidentalis* (Nutt.) T. & G.—Common in the streamside forest. Occasional under willows in the streambeds.

*Balsamorrhiza sagittata* (Pursh) Nutt.—Abundant in the big sagebrush community. Common under aspen on hillsides.

*Chrysopsis villosa* (Hook.) Nutt.—Occasional in streambeds.

*Cirsium arvense* L.—Common in waste places.

*Cirsium drummondii* T. & G.—Common in the intervale and silver sagebrush community. Occasional in the streamside forest and under aspen on hillsides.

*Conyza canadensis* (L.) Cronq.—Occasional in waste places.

*Crepis acuminata* Nutt.—Occasional in streambeds and under lodgepole pine.

*Crepis intermedia* Gray.—Common in the big sagebrush community.

*Crepis tectorum* L.—Common along drier parts of streambeds.

*Erigeron divergens* T. & G.—Common in the streamside forest and big sagebrush community.

*Erigeron glabellus* Nutt.—Common in the sedge-grass meadow, along streambeds, and in the streamside forest.

*Erigeron lonchophyllus* Hook.—Occasional in the intervale.

*Erigeron ochroleucus* Nutt.—Common in the big sagebrush community.

*Erigeron pumilus* Nutt. ssp. *concinnoides* Cronq.—Common in the big sagebrush community.

*Erigeron speciosus* (Lindl.) DC. var. *macranthus* (Nutt.) Cronq.—Abundant under aspen on hillsides and in the big sagebrush community. Common under lodgepole pine.

*Eriophyllum lanatum* (Pursh) Forbes var. *integrifolium* (Hook.) Smiley.—Abundant in the big sagebrush community and in the lodgepole pine forest. Common in the intervale and in the silver sagebrush community.

*Gnaphalium chilense* Spreng.—Occasional in sand of streambeds.

*Gnaphalium palustre* Nutt.—Abundant on wet mud and on wet sand in streambeds.

*Grindelia squarrosa* (Pursh) Duval.—Common in waste places.

*Helianthella quinquenervis* (Hook.) Gray.—Abundant in aspen stands. Common in the streamside forest. Occasional under lodgepole pine.

*Hieracium albiflorum* Hook.—Abundant under lodgepole pine.

*Hieracium cynoglossoides* Arn.—Occasional under lodgepole pine.

*Hieracium scouleri* Hook.—Abundant under the coniferous canopies. Common under aspen on hillsides. Occasional in the intervale and in both sagebrush communities.

*Iva xanthifolia* Nutt.—Common in waste places.

*Lactuca integrata* (Gren. & Godr.) A. Nels.—Common along streambeds and in waste places.

*Machaeranthera pulverulenta* (Nutt.) Greene.—Abundant in the big sagebrush community.

*Machaeranthera viscosa* (Nutt.) Greene.—Occasional in waste places.

*Madia glomerata* Hook.—Abundant in waste places.

*Matricaria suaveolens* (Pursh) Buch.—Common in waste places.

*Rudbeckia occidentalis* Nutt.—Occasional at the edges of moist aspen groves.

*Senecio cymbalarioides* Nutt.—Common in the streamside forest.

*Senecio glaucescens* Rydb.—Occasional in the big sagebrush community.

*Senecio hydrophilus* Nutt.—Occasional on wet sod and in the sedge meadow.

*Senecio perplexus* A. Nels.—Abundant in the intervale and in both sagebrush communities.

*Senecio serra* Hook.—Abundant in moist aspen groves. Occasional under aspen on hillsides and in the big sagebrush community.

*Solidago lepida* DC. var. *elongata* (Nutt.) Fern.—Common in the streamside forest and in moist aspen groves. Occasional in the streambeds.

*Solidago lepida* DC. var. *fallax* Fern.—Abundant under aspen on moist sites. Common in the shrub-swamps, along streambeds, in the streamside forest, and in both sagebrush communities.

*Solidago missouriensis* Nutt.—Common in the streamside forest.

*Solidago nemoralis* Ait.—Common in the intervale.

*Stephanomeria tenuifolia* (Torr.) Hall.—Common on wet sand in streambeds.

*Tanacetum vulgare* L.—Remaining from previous cultivation.

*Taraxacum officinale* Weber.—Very abundant in the intervale and in the big sagebrush community. Abundant in aspen stands, in the silver sagebrush community, under lodgepole pine, and in waste places. Common in the streamside forest and sedge-grass meadow.

*Tetradymia inermis* Nutt.—Locally common in the big sagebrush community.

*Tragopogon porrifolius* L.—Common in waste places, the intervale, and in the big sagebrush community. Occasional under aspen on hillsides.

*Viguiera mutiflora* (Nutt.) Blake.—Abundant under aspen on hillsides. Common in the big sagebrush community.

*Wyethia helianthoides* Nutt.—Rare in the sedge-grass meadow.

# The Effect of Precipitation and Temperature Upon the Radial Growth of Red Pine

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Foresters and ecologists have for decades attempted to determine just what influence climate has on tree growth. Two of the most frequently studied facets in climate are precipitation and temperature. For the past three years dendrometer growth records have been made on a 22-year-old red pine, *Pinus resinosa* Ait., plantation on the Dunbar Forest, Chippewa County, Michigan. These data indicate a close correlation between precipitation and radial growth in red pine. Temperature appears to influence this growth mainly through its effect upon the length of the growing season.

Since May 1948 growth measurements have been taken at least once a week during the growing season with the dial-gauge dendrometer as described by Daubenmire.[1] Data furnished herein represent the average for 10 trees selected as being representative. Weather data have been taken from observations made at the Dunbar Forest Experiment Station, a cooperating U. S. Weather Bureau station.

Figures 1-3 show cumulative growth in radius, mean daily temperature and daily precipitation for the growing seasons 1948 through 1950. Figure 4 shows the cumulative growth and precipitation curves for the three seasons. Table 1 shows monthly precipitation and growth summaries for June, July, and August for three years.

*Precipitation.*—Precipitation appears to be very closely related to radial growth in red pine. In examining the precipitation and growth curves in figures 1-3 it is noted that prolonged dry weather is accompanied by a leveling-off tendency in the growth curve. The growth curve starts climbing immediately following a period of significant rainfall.

The entire growing season of 1948 was considerably below average in the amount of precipitation received. In 1949 and 1950 precipitation was about average or a little above average. A comparison of the three growth curves in figure 4 shows total growth in 1948 to be only a little over half that of 1950.

The spring of 1948 was exceptionally dry. Rainfall from May 6 to June 22, a period of over 6 weeks, was practically negligible. The growth curve over this period is comparatively flat. On June 22, 23, and 24 there was nearly an inch and a half of rainfall. Following this the growth currve started

1 Daubenmire, R. F. 1945—An improved type of precision dendrometer. Ecology (26)1:97-98.

a sharp climb. On June 21 it was noted that orange hawkweed, *Hieracium aurantiacum* L., growing in openings and on the edges of the plantation had started to wilt. This would indicate that the soil moisture was very near the wilting point. Again in the middle of July there was a moisture deficiency which shows up in the flattening of the growth curve. From July 19 to August 1 over an inch and three quarters of rain fell and radial growth started upward again.

TABLE 1.—Monthly radial growth, precipitation and departure from normal summaries

| Month | Growth in .001 inches | Departure from normal in .001 inches | Precipitation in inches | Departure from normal in inches |
|---|---|---|---|---|
| | | 1948 | | |
| June | 24 | —33 | 2.10 | —1.61 |
| July | 25 | —15 | 2.38 | —0.31 |
| August | 18 | 0 | 1.97 | —0.73 |
| Totals | 67 | —48 | 6.45 | —2.65 |
| | | 1949 | | |
| June | 81 | +24 | 4.53 | +0.82 |
| July | 56 | +16 | 3.44 | +0.75 |
| August | 21 | +3 | 1.56 | —1.14 |
| Totals | 158 | +43 | 9.53 | +0.43 |
| | | 1950 | | |
| June | 65 | +8 | 3.94 | +0.23 |
| July | 40 | 0 | 1.39 | —1.30 |
| August | 15 | —3 | 2.34 | —0.36 |
| Totals | 120 | +5 | 7.67 | —0.43 |

In the latter part of August 1948, the growth curve shows a decrease. This was probably caused by a combination of the precipitation and temperature elements. For nearly a week the weather was hot and dry causing excessive transpiration and evaporation which resulted in shrinkage in the bark and cambium. This same situation occurred to a lesser extent in late August and early September of 1949. It is quite possible that such erratic growth is more closely associated with the approach of the end of the growing season rather than with the precipitation and temperature factors.

Precipitation records show that rainfall for May, June, and July in 1949 was 18 per cent above normal while in August 1949, rainfall was about 40 per cent below normal. This, too, is apparent in the growth curve which shows total growth in 1949 to be more than twice that of 1948. A slight decrease in growth in the latter part of August is indicated which may be the result of the low rainfall in August.

The trend of the 1950 growth curve is very similar to that of 1949 for the month of June. In July 1950, however, precipitation was nearly 50 per cent below normal. This is reflected in the growth curve which shows a marked trend downward.

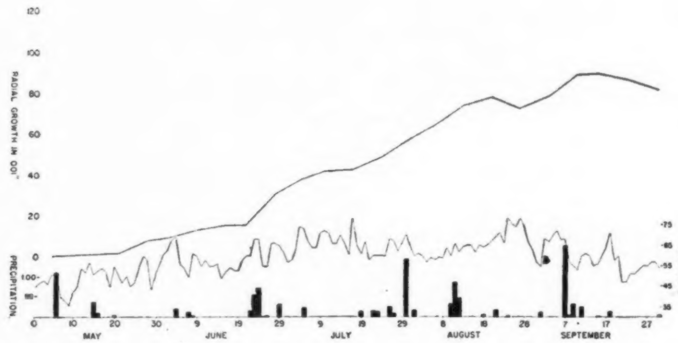


Fig. 1.—Red pine radial growth, precipitation and temperature records for 1948

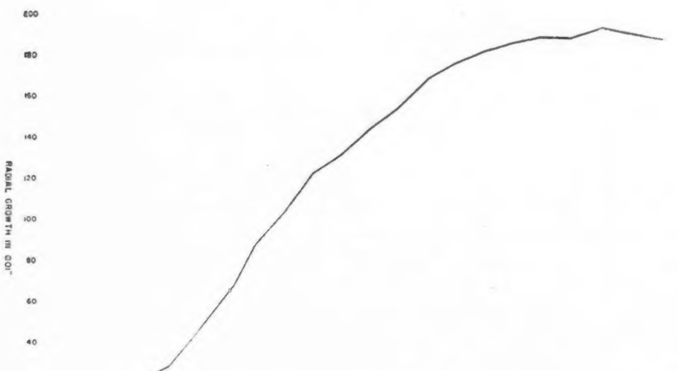


Fig. 2.—Red pine radial growth, precipitation and temperature records for 1949

*Temperature.*—Mean daily temperature does not appear to be so closely related to radial growth in red pine as is precipitation. Mean daily temperature as well as growth and precipitation curves are given in figures 1-3.

The dates of the last killing frosts in spring were May 25, May 25, and May 19 for 1948, 1949, and 1950 respectively. Although the last killing frost came 6 days earlier in 1950 than in 1949 the growing season, as indicated on the growth curves, actually started 7 to 10 days later. Since precipitation for the spring of 1950 was only slightly less than in 1949, this delaying of the growing season is apparently an influence of temperature. The temperature curve for 1950 starts considerably lower than those of the two previous years.

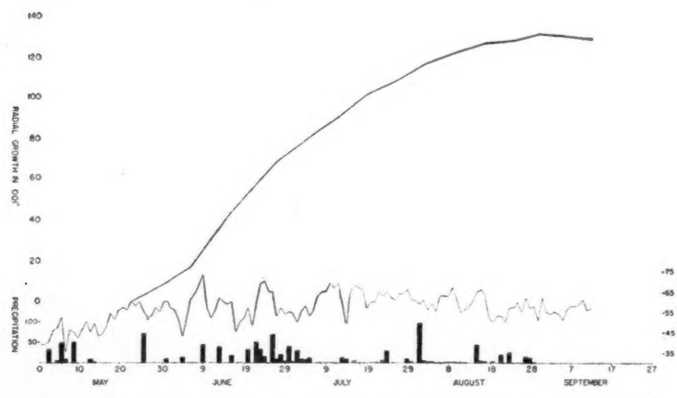


Fig. 3.—Red pine radial growth, precipitation and temperature records for 1950

The spring of 1950 was unusually cold. There was a snow cover on the ground until May 1 and weather records show that the mean temperature for the month of May was over 6 per cent below normal.

The minimum temperatures on the dates of the last killing frosts were 30, 31, and 31 degrees Fahrenheit for 1948, 1949, and 1950 respectively. The growth curves do not show a slowing up in growth following these frosts.

Variations in temperature failed to show a close relationship with growth in diameter in red pine except as noted above.

*Conclusions.*—Amount of radial growth seems to be attendant upon the presence of a surplus of soil moisture. This is particularly true during the earlier part of the growing season but any period of 10 days to 2 weeks or more without rainfall is usually accompanied by a diminishing in the radial

growth. The date of the beginning of the growing season appears to be primarily a function of temperature. Minor variations in temperature during the growing season, however, failed to indicate any marked relationship with radial growth.

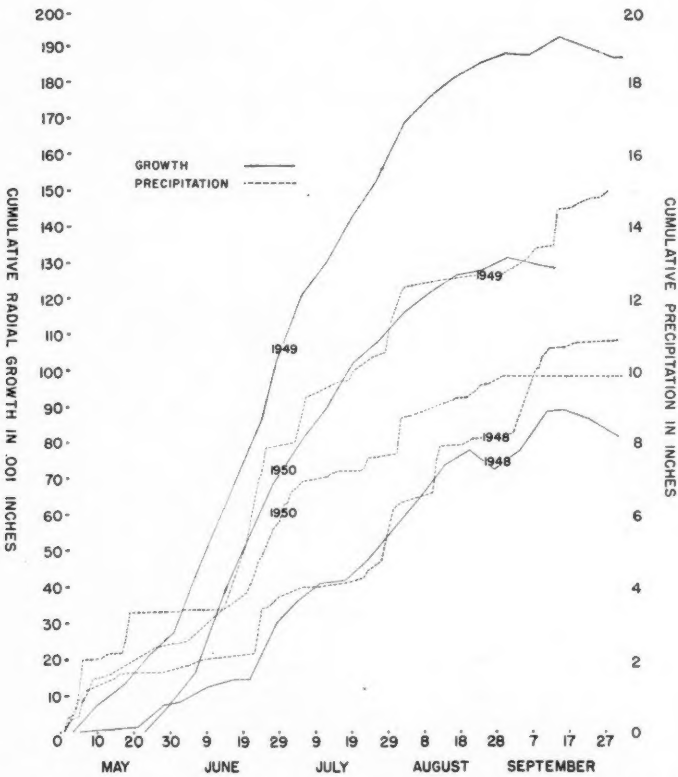


Fig. 4.—Cumulative red pine growth and precipitation curves for 1948 to 1950

# List of Non-Vascular Plants From Ponape, Caroline Islands

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During the summer of 1949, the writer collected 500 numbers of plants from the island of Ponape, the largest of the eastern Caroline Islands. Approximately 75 of these were non-vascular plants. The vascular flora of Ponape has already been treated in a recent paper by the writer (1952). The present work, however, appears to be the first attempt to list all available records of non-vascular plants occurring on the island.

Apparently, the first record of a non-vascular plant from Ponape was reported by Jatta (1903) who cited a lichen collected by Parkinson. In 1921, Sydow and Sydow listed a number of fungi, and Schmidt cited some algae in 1928. In both instances, citations were based on collections made by Ledermann between 1913 and 1914. Specimens of algae collected by Koshida in 1914 and Yanagi in 1915 were cited by Okamura (1916). Bartram (1945) wrote a short paper on mosses collected by Takamatsu in 1936, and Imazeki (1941) cited some fungi collected on the island by Huzii in 1915, Kobayasi in 1936, and Esaki in 1939. In 1939 Kobayasi wrote an article on the fungi of Ponape based on his collections. Sakurai (1943) cited a number of mosses collected by Kondo and Okabe in 1941. Horikawa (1949) listed some bryophytes which he collected in 1940, and Tanaka included some algae from Ponape in 1944.

In the following list, 178 species, varieties and forms are enumerated. Of this total 60 are algae, 47 fungi, 9 lichens, 49 mosses, and 13 liverworts. Entries are based either on the writer's collections, on a few collections of F. R. Fosberg deposited in the Chicago Natural History Museum or in the personal herbarium of Fosberg, or on names of species from Ponape published in taxonomic articles. Most of the specimens cited were determined by the following specialists to whom the writer is most grateful: Dr. F. Drouet, Chicago Natural History Museum, all algae except diatoms which were identified by Dr. R. Patrick, Academy of Natural Sciences, Philadelphia; Dr. C. W. Dodge, Missouri Botanical Garden, lichens; Mr. E. B. Bartram, Bushkill, Penn., mosses; and Dr. M. Fulford, University of Cincinnati, liverworts. The writer's personal collection of Ponape fungi have not been determined as yet. A set of specimens for each respective group has been distributed to the above-mentioned herbaria, and one complete set is deposited in the Cryptogamic Herbarium of the Chicago Natural History Museum. Additional sets will be distributed at a future date. Authorities for determinations of Fosberg's specimens are indicated in each instance.

## List of Species

### Algae

(Diatoms are indicated by an asterisk)

*Acanthophora orientalis* J. Ag.; Okamura, Bot. Mag. Tokyo 30: 11. 1916.
*Calothrix crustacea* Born. & Flah., 2301a, Metalanim District, June 20.
*Caulerpa boryana* Harv.; Okamura, loc. cit. 2.
*Caulerpa cupressoides* var. *typica* (Vahl) Weber; Okamura, loc. cit. 3.
*Caulerpa freycinetti* Ag. var. *boryana* (J. Ag.) Weber; Schmidt, Hedwigia 68: 35. 1928.
*Caulerpa okamurai* Weber; Okamura, loc. cit. 4; Schmidt, loc. cit. 36.
*Caulerpa plumeris* (Forsk.) Ag.; Schmidt, loc. cit. 34.
*Caulerpa plumeris* forma *brevipes* (J. Ag.) Weber; Okamura, loc. cit. 3.
*Caulerpa racemosa* (Forsk.) Weber var. *chemnitzia* (Esp.) Weber; Okamura, loc. cit. 3; Schmidt, loc. cit. 37.
*Caulerpa racemosa* var. *clavifera* (Turn.) Weber; Schmidt, loc. cit. 36.
*Caulerpa racemosa* var. *clavifera* forma *macrophysa* Weber; Okamura, loc. cit. 3.
*Ceramium clavulatum* Ag.; Okamura, Bot. Mag. Tokyo 30: 3. 1916.
*Champia parvula* (Ag.) J. Ag.; Okamura, loc. cit. 10; Schmidt, Hedwigia 68: 65. 1928.
*Chlorodesmis comosa* Bail. & Harv.; Schmidt, loc. cit. 38.
*Chlorodesmis hildebrandtii* A. & E. S. Gepp; Okamura, loc. cit. 4; Schmidt, loc. cit. 38.
*Cladophora patentiramea* (Mont.) Kutz.; Schmidt, loc. cit. 28.
*Closterium lunula* var. *massartii* (de Wildem.) Kruger, 2577, vicinity of Colonia, in pond, abundant, July 20.
*Colpomenia sinuosa* (Roth) Derb. & Sol.; Okamura, loc. cit. 6; Schmidt, loc. cit. 44.
*Corallopsis minor* (Sond.) J. Ag.; Schmidt, loc. cit. 64.
*Dictyonema membranaceum* Ag., 2505, Mt. Poaipoai, 2000 ft., rain forest, epiphyte, common, July 9.
*Dictyota* sp.; Okamura, loc. cit. 3.
*Dictyota patens* J. Ag.; Schmidt, loc. cit. 53.
*Dilophus radicans* Okamura; Schmidt, loc. cit. 54.
*Euglena* sp., 2762, Metalanim District, floating in ditch, Aug. 2, 2459, *Ronkiti*, roadside ditch, July 7.
*Entophysalis brebissonii* (Menegh.) Dr. & Dailey., 2763, Metalanim District, on tree roots in Sapalap River, Aug. 2.
*Erythrotrichia carnea* (Dillwyn) J. Ag. forma *tenuis* Tanaka, Sci. Pap. Inst. Algol. Hokkaido 3: 92. 1944.
*Floribundaria floribunda* (D. & M.) Fl., 2311, Mt. Peipalap, 800 ft., on moist rocks, June 22.
**Frustulia rhomboides* (Ehrenb.) de Toni., 2347, Mt. Tamatamansakir, 1000 ft., rain forest, in puddle, June 23.
*Goniotrichum alsidii* (Zanardini) Howe; Tanaka, Journ. Jap. Bot. 20: 217. 1944.
*Gracilaria* sp., 2303, 2303a, Metalanim District, in mangrove swamp, June 20.
*Halarachnion calcareum* Okamura, Bot. Mag. Tokyo 30: 13. 1916; Schmidt, Hedwigia 68: 77. 1928.
*Halimeda cuneata* Hering forma *digitata* Barton; Okamura, loc. cit. 4; Schmidt, loc. cit. 40.
*Halimeda macroloba* Decne.; Okamura, loc. cit. 4; Schmidt, loc. cit. 40.
*Halimeda opuntia* (L.) Lamx.; Schmidt, loc. ict. 40, 2302, Metalanim District, Mangrove swamp, June 20.
*Halimeda opuntia* forma *triloba* Decne.; Okamura, loc. cit. 4.
*Halimeda tuna* (Ell. & Sol.) Lamx., 2302b, Metalanim District, mangrove swamp, June 20.
**Hantzchia amphioxys* (Ehrenb.) Grun., 2319, Jokaj, in mud puddle, June 22.
*Hydroclathrus cancellatus* Bory; Okamura, Bot. Mag. Tokyo 30: 6. 1916; Schmidt, Hedwigia 68: 44. 1928.
*Hypnea pannosa* J. Ag.; Okamura, loc. cit. 10.
*Laurencia intricata* Lamx.; Okamura, loc. cit. 11.

*Leveillea jungermannioides* (Mart. & Hering) Harv.; Okamura, loc. cit. 11.
*Lyngbya lutea* Gom., 2301, Metalanim District, mangrove swamp, June 20.
**Navicula* sp., 2319, Jokaj, in mud puddle, June 22.
*Oedogonium* sp., 2347, Mt. Tamatamansakir, rain forest, 1200 ft., June 23; 2577, vicinity of Colonia, in pond, July 20; 2763, Metalanim District, Sapalap, on tree roots in water, Aug. 2.
*Oscillatoria tenuis* Gom., 2731, Mt. Seletereh, 1350 ft., rain forest, in mud puddle, July 28.
*Padina pavonina* (L.) Lamx.; Okamura, loc. cit. 9.
*Pithophora oedogonia* (Mont.) Wittr., 2763a, Metalanim District, on tree roots in Sapalap River, Aug. 2.
*Rhizoclonium hieroglyphicum* (Ag.) Kutz., 2318, Mt. Peipalap, 300 ft., in mud puddle, June 22.
*Roschera glomerulata* (Ag.) Weber; Okamura, Bot. Mag. Tokyo 30: 11. 1916.
*Sargassum cristaefolium* Ag.; Okamura, loc. cit. 7.
*Sargassum ilicifolium* Turn., 2302a, Metalanim District, mangrove swamp, June 20.
*Scytonema guyanense* Born. & Flah., 2558, Agr. Exp. Sta. grounds, on clay bank, July 16.
*Scytonema hofmannii* Born. & Flah., 2512, vicinity of Colonia, mangrove swamp, on dead stump, July 11.
*Spongocladia vaucheriaeformis* Aresch.; Okamura, loc. cit. 5; Schmidt, Hedwigia 68: 31. 1928.
*Symploca muscorum* Gom., 2349, Agr. Exp. Sta. grounds, on brown soil, June 24.
*Trentepohila elongata* (Zell.) de Toni., 2576, Mt. Tolenkiup, 1650 ft., on stone ledge, abundant, July 14.
*Turbinaria ornata* (Turn.) J. Ag.; Okamura, loc. cit. 7; Schmidt, loc. cit. 46.
*Tydemania expeditionis* Weber; Okamura, loc. cit. 5.
*Valonia aegagrophila* (Roth) Ag.; Schmidt, loc. cit. 26.

## FUNGI

*Cyphella ledermannii* Sydow, Engl. Bot. Jahrb. 56: 431. 1921.
*Echinophallus lauterbachii* P. Henn. var. *ponapensis* Kobayasi, Bot. Mag. Tokyo 51: 749. 1937.
*Fomes lignosus* (Kl.) Bres.; Sydow, loc. cit. 431.
*Fomes setulosus* Lloyd; Imazeki, Journ. Jap. Bot. 17: 177. 1941.
*Ganoderma applanatus* (Pers. ex Fr.) Pat.; Imazeki, loc. cit. 177.
*Ganoderma boninense* Pat.; Imazeki, loc. cit. 178.
*Ganoderma fornicatum* (Fr.) Pat.; Imazeki, loc. cit. 178.
*Geastrum mirabile* (Mont.) Fischer; Kobayasi, loc. cit. 799.
*Gloeoporus dichrous* (Fr.) Bres.; Imazeki, loc. cit. 178.
*Hexagonia thwaitesii* Berk.; Sydow, loc. cit. 431.
*Hexagonia tenuis* (Hook.) Fr.; Imazeki, Journ. Jap. Bot. 17: 178. 1941.
*Hirneola polytricha* (Mont.) Fr.; Kobayasi, Bot. Mag. Tokyo 51: 803. 1937; Imazeki, loc. cit. 175.
*Hirneola porphyrea* (Lev.) Fr.; Sydow, Engl. Bot. Jahrb. 56: 431. 1921.
*Hypoxylon rubiginosum* (Pers.) Fr. Sydow, loc. cit. 432.
*Lachnea scutellata* (L.) Gill.; Sydow, loc. cit. 432.
*Lentinus palauensis* Imazeki, Journ. Jap. Bot. 17: 182, figs. 5-7. 1941.
*Lentinus tigrinus* (Bull.) Fr.; Sydow, loc. cit. 430.
*Lentinus tuber-regium* Fr.; Kusano, Journ. Jap. Bot. 5: 214-216. 1928; Imazeki, loc. cit. 184. Fosberg 26307 (Det. J. A. Stevenson).
*Lentinus velutinus* Fr.; Imazeki, loc. cit. 184.
*Linospora pandani* Sydow, Engl. Bot. Jahrb. 56: 432. 1921.
*Lycoperdon subincarnatum* Peck; Kobayasi, Bot. Mag. Tokyo 51: 802. 1937.
*Marasmius calobates* Kalchbr.; Sydow, loc. cit. 430.
*Marasmius calobates* forma *brevipoda* Sydow, Engl. Bot. Jahrb. 56: 430. 1921.
*Marasmius ramealis* (Bull.) Fr.; Sydow, loc. cit. 430.

*Megalonectria pseudotricha* (Schw.) Speg.; Sydow, loc. cit. 432; Kobayasi, Bot. Mag. Tokyo 53: 158. 1939.
*Meliola dolobrata* Sydow, Engl. Bot. Jahrb. 56: 431. 1921.
*Mycena cyanophos* Berk. & Curt. forma *carolinensis* Kobayasi, Bot. Mag. Tokyo 53: 161. 1939.
*Panus torulosus* Pers. ex Fr.; Imazeki, loc. cit. 184.
*Phialea aurantiaca* Sydow, loc. cit. 432.
*Pleurotus leptogrammus* B. & Br.; Sydow, loc. cit. 432.
*Polyporus fiji* Lloyd; Imazeki, loc. cit. 178.
*Polyporus flabelliformis* Kl., Fosberg 26467, above Nanpil, on rotting wood, Aug. 13, 1946 (Det. J. A. Stevenson).
*Polyporus grammocephalus* Berk.; Sydow, Engl. Bot. Jahrb. 56: 430. 1921; Imazeki, Journ. Jap. Bot. 17: 179. 1941.
*Polyporus mikawai* Lloyd; Imazeki, loc. cit. 179.
*Polyporus versisporus* Lloyd; Imazeki, loc. cit. 180.
*Polyporus zonalis* Berk.; Imazeki, loc. cit. 180.
*Polystictus flabelliformis* (Kl.) Fr.; Imazeki, loc. cit. 180.
*Polystictus hirsutus* (Wulf ex Fr.) Saccardo; Imazeki, loc. cit. 180.
*Polystictus meleagris* (Berk.) Saccardo; Sydow, loc. cit. 431; Imazeki, loc. cit. 181.
*Polystictus microloma* (Lev.) Cke.; Sydow, loc. cit. 431.
*Polystictus sanguineus* L. ex Fr.; Imazeki, loc. cit. 182.
*Schizophyllum commune* Fr.; Sydow, loc. cit. 430.
*Stereum surinamense* Lev.; Imazeki, loc. cit. 176.
*Stilbella cinnabarina* (Mont.) Lindau; Sydow, loc. cit. 432.
*Trametes corrugata* (Pers.) Bres.; Imazeki, loc. cit. 182.
*Trametes tricolor* Lloyd; Imazeki, loc. cit. 182.
*Ustilaginoidea ochracea* P. Henn.; Sydow, loc. cit. 432.

## LICHENS

*Leptogium azureum* (Sw.) Nyl. var. *laevius* Wain., 2881a, Mt. Nanalaut, 2200 ft., rain forest, Aug. 17.
*Leptogium caesium* (Ach.) Wain.; Jatta, Malpighia 17: 15. 1903.
*Pannaria mariana* (Fr.) Muell. Arg., 2489, Mt. Poaipoai, 1600 ft., rain forest, July 8.
*Phyllopsora furfuracea* (Pers.) Zahlbr., 2390a, Mt. Nanalaut, 1600 ft., rain forest, June 28.
*Physma boryanum* (Pers.) Mass., 2489a, Mt. Poaipoai, 1600 ft., rain forest, July 8.
*Physma plumbeum* (Schaer) Dodge, 2390, Mt. Nanalaut, 1600 ft., rain forest, June 28.
*Pseudocyphellaria dissimulata* var. *inaequalis* Zahlbr., 2344, Mt. Tamatamansakir, 1300 ft., June 23.
*Sticta beccari* Krmph., 2344a, Mt. Tamatamansakir, 1300 ft., June 23; 2390b, Mt. Nanalaut, 1600 ft., rain forest, June 28.
*Sticta dichotoma* Bory., Fosberg 26417, Tolun Nanket, 600 m., on tree trunk, Aug. 13, 1946 (Det. W. W. Diehl).

## MOSSES

*Acanthorynchium papillatum* (Harv.) Fl.; Sakurai, Bot. Mag. Tokyo 57: 252. 1943., 2335d, 2346c, Mt. Tamatamansakir, 1000 ft., rain forest, epiphyte, June 23.
*Acromastigum capillare* (Stephani) Evans; Horikawa, Journ. Jap. Bot. 24: 140. 1949.
*Acroporium brevisetulum* (C.M.) Jaeg.; Bartr., Bryologist 48: 51. 1945.
*Aerobryopsis longissima* (D.M.) Fl.; Sakurai, loc. cit. 254.
*Barbella pendula* (Sull.) Fl.; Sakurai, loc. cit. 92.
*Calymperes orientale* Mitt.; Sakurai, loc. cit. 90.
*Calymperes serratum* Al. Br.; Bartr., loc. cit. 49., 2493, Mt. Poaipoai, 1700 ft., rain forest, common epiphyte, July 8.
*Campylopus umbellatus* (W. Arn.) Bartr., 2887b, Mt. Ninani, 2550 ft., terrestrial and epiphytic, on wind blown peak associated with dwarf trees, Aug. 17.
*Dicranella ponapensis* Sakurai, Bot. Mag. Tokyo 57: 86, fig. 1. 1943.

*Distichophyllum cuspidatum* D.M.; Sakurai, loc. cit. 255.

*Distichophyllum undulatum* Bosch & Sande; Horikawa, Journ. Jap. Bot. 24: 143. 1949.

*Ectropothecium diversirete* Bartr.; Bartr., Bryologist 48: 51. 1945., 2311a, Mt. Peipalap, 500 ft., on moist rocks, June 22.

*Ectropothecium hyalinum* (Hirsch & Rw.) Fl.; Sakurai, loc. cit. 253.

*Ectropothecium ponapense* Bartr., loc. cit. 51., 2887a, Mt. Ninani, 2550 ft., terrestrial and epiphytic, on wind blown peak associated with dwarf trees, Aug. 17.

*Ectropothecium sparsipilum* (v.d. Bosch & Lac.) Jaeg.; Sakurai, loc. cit. 253.

*Endotrichella elegans* (D.M.) Fl.; Sakurai, loc. cit. 92., 2488, Mt. Poaipoai, 1700 ft., rain forest, July 8.

*Endotrichella nematosa* Bartr.; Bartr., Bryologist 48: 50. 1945.

*Exodictyon blumii* (C.M.) Fl.; Bartr., loc. cit. 50; Horikawa, Journ. Jap. Bot. 24: 140. 1949., 2335a, Mt. Tamatamansakir, 1000 ft., rain forest, June 23.

*Exodictyon papillosum* (Mitt.) Fl.; Sakurai, loc. cit. 87.

*Fissidens kondoi* Sakurai, Bot. Mag. Tokyo 57: 250. 1943.

*Garckea phascoides* (Hk.) C.M.; Sakurai, loc. cit. 91.

*Himantocladium loriforme* (Lac.) Fl.; Sakurai, loc. cit. 254., 2346a, Mt. Tamatamansakir, 1000 ft., rain forest, epiphyte, June 23.

*Leucobryum sanctum* Hampe; Bartr., Bryologist, 48: 50. 1945., Fosberg 26433 (det. E. B. Bartram); 2335c, Mt. Tamatamansakir, 1000 ft., rain forest, June 23; 2393c, Mt. Nanalaut, 1800 ft., June 28, 2849, Mt. Tolotom, 1750 ft., Aug. 11; 2887, Mt. Ninani, 2550 ft., terrestrial and epiphytic, in wind blown peak associated with dwarf trees.

*Leucophanella amoena* (Broth.) Fl.; Sakurai, loc. cit. 88.

*Leucophanes candidum* (Hirsch) Lindb. forma *fuscescens* Sakurai, Bot. Mag. Tokyo 57: 87. 1943.

*Leucophanes octoblepharoides* Brid., 2346b, Mt. Tamatamansakir, 1000 ft., rain forest, June 23.

*Macromitrium okabei* Sakurai, loc. cit. 250.

*Meiothecium bogoriense* Fl.; Sakurai, loc. cit. 254.

*Mniomalia semilimbata* C.M.; Sakurai, loc. cit. 90.

*Neckeropsis gracilenta* (Lac.) Fl.; Sakurai, loc. cit. 91.

*Rhacelopus ponapensis* Sakurai, Bot. Mag. Tokyo 57: 91. 1943.

*Schistomitrium apiculatum* D.M.; Sakurai, loc. cit. 87.

*Spiridens balfourianus* Grev.; Bartr., Bryologist 48: 50. 1945.

*Spiridens capilliferus* Mitt., Fosberg 26436 (det. E. B. Bartram).

*Spiridens reinwardtii* Nees; Sakurai, loc. cit. 91.

*Syrrhopodon ciliatus* (Hk.) Schw.; Sakurai, loc. cit. 90.

*Syrrhopodon croceus* Mitt.; Sakurai, loc. cit. 90., 2393b, Mt. Nanalaut, 1800 ft., rain forest, June 28.

*Syrrhopodon graeffeanus* C.M.; Bartr., loc. cit. 49.

*Syrrhopodon mulleri* (D.M.) Lac., 2335b, Mt. Tamatamansakir, 1000 ft., rain forest, June 23; 2393a, Mt. Nanalaut, 1800 ft., rain forest, June 28.

*Syrrhopodon tristichus* Nees; Sakurai, Bot. Mag. Tokyo 57: 90. 1943.

*Syrrhopodon victorianus* Bartr., 2393, Mt. Nanalaut, 1800 ft., rain forest, June 28; 2881, Mt. Nanalaut, 2200 ft., abundant epiphyte on tree trunks, Aug. 17.

*Thuidium glaucinoides* Broth.; Bartr., Bryologist 48: 50. 1945., 2346, Mt. Tamatamansakir, 1000 ft., rain forest, June 23; 2488a, Mt. Poaipoai, 1700 ft., rain forest, July 8.

*Thuidium orientale* Mitt.; Sakurai, loc. cit. 250.

*Thyridium constrictum* Mitt.; Sakurai, loc. cit. 88.

*Thyridium fasciculatum* (Hk. & Grev.) Mitt.; Sakurai, loc. cit. 88.

*Thyridium undulatum* (Lindb.) Fl.; Sakurai, Bot. Mag. Tokyo 57: 249. 1943.

*Trichostelium hamatum* (D.M.) Jaeg.; Sakurai, loc. cit. 251.

*Vesicularia dubyana* (C.M.) Broth.; Sakurai, loc. cit. 254.

*Vesicularia inflectens* (Brid.) C.M.; Bartr., Bryologist 48: 52. 1945.

*Warburgiella leptocarpa* (Schw.) Fl.; Sakurai, loc. cit. 253.

### LIVERWORTS

*Acrobolus* sp., 2388aa, Mt. Nanalaut, 1800 ft., rain forest, June 28.
*Anthoceros* sp., 2735, Mt. Seletereh, 1900 ft., rain forest, on clay soil, July 28.
*Bazzania* sp., 2881b, Mt. Nanalaut, 2200 ft., Aug. 17.
*Bazzania spirale* or *B. descisens.*, 2488b, Mt. Poaipoai, 1700 ft., rain forest, common epiphyte, July 8.
*Drepanolejeuna* sp., 2493a, Mt. Poaipoai, 1700 ft., rain forest, July 8.
*Frullania* sp., 2552, Mt. Beirut, 2100 ft., common epiphyte, July 15.
*Lopholejeuna* sp., 2311b, Mt. Peipalap, 500 ft., on moist rocks, June 20.
*Mastigophora diclados* (Brid.) Nees., 2488b, Mt. Poaipoai, 1700 ft., rain forest, July 8.
*Microlejeuna ponapensis* Horikawa, Bot. Mag. Tokyo 50: 381. 1936.
*Pleurozia gigantea* (Web.) Lindb., 2393e, Mt. Nanalaut, 1800 ft., rain forest, June 28.
*Radula* sp., 2346e, Mt. Tamatamansakir, 1000 ft., rain forest, June 23.
*Symphyogyna* sp., 2538, Mt. Tolenkiup, 1700 ft., rain forest, July 15.
*Thysananthus comosus* Lindb., 2393d, Mt. Nanalaut, 1800 ft., rain forest, June 28.

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# Notes on Wisconsin Parasitic Fungi. XVI.

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This series of notes includes a considerable number of items based on a study of the last of the extensive unworked material left by the late J. J. Davis, who collected the plant parasitic fungi of Wisconsin over the period 1890-1936. Other notes and descriptions are concerned principally with collections made during the season of 1951, and the year date is omitted in such case.

Unidentified powdery mildews have been noted on: *Rubus canadensis,* Vilas Co., Woodruff, August 10, 1936. Coll. J. J. Davis; *Ratibida* (*Lepachys*) *pinnata,* Grant Co., Elmo, July 30; on *Asclepias amplexicaulis,* Dane Co., Madison, August 26; on *Solidago speciosa,* Dane Co., Madison, August 29; on the ray flowers of *Brauneria* (*Echinacea*) *purpurea,* but not on the leaves, Dane Co., Madison, September 1.

PHYSALOSPORA sp. on leaves of *Oryzopsis asperifolia,* collected in October 1920 at Fish Creek, Door Co., by J. J. Davis is, in its microscopic characters, unlike other species described on Gramineae. The subglobose perithecia are about 250- 300 $\mu$ diam., the asci relatively very wide, approx. 60 x 20 $\mu$, but becoming much narrowed at the base. The ascospores are subdistichous, entirely filling the ascus, smooth, 23-25 x 6 $\mu$. Of questionable parsitism, but appearing to have developed on the current season's leaves.

MYCOSPHAERELLA species, largely indeterminate, are occasionally found on living foliage of various plants, acting evidently as parasites and without any demonstrable connection with an imperfect stage. The following are in this category: 1) On leaves of *Selaginella rupestris,* coll. J. J. Davis near Muscoda, Grant Co., October 7, 1936. The crowded perithecia are black, globose, 55-75 $\mu$ diam., the broadly clavate asci are 13 x 23 $\mu$, and the hyaline ascospores are subfusoid, 16-18 x 4 $\mu$; 2) On fronds of *Dryopteris spinulosa* coll. by Davis at Hixton, Jackson Co., September 3, 1917. The asci are short-clavate, about 35 x 10 $\mu$, the ascospores 10-12 x 3 $\mu$. In dimensions this is similar to an undetermined species of *Mycosphaerella* recently collected on *Botrychium virginianum,* but the latter matured only after overwintering on the dead leaves. On *Dryopteris* the infected areas are closely beset with the perithecia and have turned brown, but the adjacent tissue has remained green; 3) On leaves of *Oryzopsis asperifolia* coll. by Davis near Phillips, Price Co., September 19, 1911. Mixed with immature *Phyllachora oryzopsidis.* The perithecia are scattered, innate, subglobose, black, thin-walled, 100-140 $\mu$ diam., the asci cylindrical to clavate-cylindrical, short-pedicellate, 50-75 x 13-16 $\mu$, the ascospores fusoid-oblong, slightly constricted at septum, crowded in ascus, hyaline, 23-27 x 4-6 $\mu$; 4) On the dying tips of young and otherwise vigorously developing leaves of *Andropogon furcatus* at Madison, May 25. The leaf tips are closely studded with the small black perithecia, which are pseudo-

parenchymatous, widely ostiolate, about 75-100 μ diam., while the asci are obclavate with a very well-defined short pedicel, 45-50 x 10 μ, with ascospores hyaline, subcylindric, 12 x 3.5 μ.

OPHIOBOLUS (GRAMINIS Sacc.?) on *Bromus inermis*. Dane Co., Madison University of Wisconsin Hill Farm, October 1950. Coll. & det. J. G. Dickson. The fungus came to maturity on plants brought into the greenhouse over winter.

ROSENSCHELDIA HELIOPSIDIS (Schw.) Theiss. & Syd., on leaves of *Helianthus rigidus*, collected June 28 at Madison, shows profuse production of rod-shaped microconidia, about 4 x 1.5 μ. Current season developments of this organism seen by me previously have been sterile, or have had large, subglobose, *Phyllosticta*-type conidia.

MOLLISIA sp. occurred on dead upper portions of leaves of *Pinus strobus* in a plantation in the University of Wisconsin Arboretum at Madison in May. The tree is one of a number which, over a period of years, have grown poorly and which have many less than the usual number of needle clusters. The following notes were made: Apothecia superficial, sessile, rounded to subhysteriform, edges inrolled, small, the largest about 250-300 μ diam., exciple dull brown; paraphyses filiform with slightly inflated tips, 80-90 x 2.5-3 μ, forming an epithecium; asci 60-75 x 10 μ; ascospores fusoid-elliptic, 16-17 x 4 μ. Parasitism doubtful.

LEPTOSPHAERIA sp. occurs on spots on leaves of *Populus deltoides*, collected by J. J. Davis, August 4, 1914 at Bridgeport near Prairie du Chien. The spots are rounded or broadly elliptic, 4-5 mm. diam., on the upper leaf surface, dull purplish with a narrow darker margin, on the lower surface paler with a more distinct margin. The black subglobose perithecia are epiphyllous, about 100 μ diam. The asci are about 45 x 10 μ, subelliptic, with a short but distinct pedicel. The fusoid ascospores are olivaceous, 15 x 3 μ, 4-septate. The spots do not appear to have resulted from insect attack and are sharply delimited from the rest of the leaf, so it seems probable that the *Leptosphaeria* was the primary agent.

DARLUCA FILUM (Biv.) Cast., the uredinicolous parasite, is said by P. D. Keener (Pl. Dis. Rept. 35:86. 1951) to have developed an ascigerous stage in material collected by him in Pennsylvania. Ascospore cultures on lima bean agar produced typical *Darluca filum* pycnidia and conidia. Keener points out that *Eudarluca* Speg. is probably the name that should be applied to the ascigerous stage.

*Taxus canadensis* is not included as a host for any parasites in the Wisconsin lists, which is somewhat misleading, for the living foliage is commonly severely blighted by a fungus which produces abundant black, globose, epiphyllous, subepidermal bodies which I assume are immature perithecia that require overwintering for complete development. It seems highly probable that the fungus is *Sphaerulina taxicola* (Pk.) Berl., for the Wisconsin collections are macroscopically identical with European material distributed as that species.

PUCCINIA SILPHII Schw. is sometimes qiute damaging to *Silphium integrifolium* in Wisconsin and occurs on all four of our species. The ultimate in destructiveness, however, was noted in July 1951 on remnants of the Rock Prairie near Janesville, where very old and large plants of *Silphium laciniatum* had been killed back to the ground. The massively infected leaves and stunted flower stalks lay prostrate in reddish-brown heaps.

PILEOLARIA TOXICODENDRI (Berk. & Rav.) Arth. is one of the rusts having uredinoid aecia. A specimen collected at Tower Hill State Park, Iowa Co., in June 1949 is the only Wisconsin material to date which shows this stage.

UROMYCES JUNCI (Desm.) Tul. was reported in the account in North American Flora to have its aecial stage on *Helianthus strumosus* in Wisconsin. In Arthur's Manual, however, this was shifted to *Uromyces silphii* (Burr.) Arth. (*U. junci-tenuis* Syd.). Uredia and telia of *U. junci* have not been reported for Wisconsin. Aecial specimens collected, but not reported, by Davis on *Helianthus occidentalis* at Millston, Jackson Co., in 1936, are provisionally referred on the basis of spore size and host to *Uromyces junci*. Iowa is the sole locality given in Arthur's Manual for this rust on *H. occidentalis*.

*Asclepias phytolaccoides* has been noted on two occasions, at Devils Lake and more recently at Madison, bearing well-developed pycnia, but no mature aecia of a so far undetermined rust, perhaps *Puccinia seymouriana* Arth.

PUCCINIA VEXANS Farl. I appears (Trans. Wis. Acad. Sci. 35:123. 1944) on a phanerogamic specimen of *Acerates viridiflora* var. *lanceolata* collected ninety years ago at Madison. The first subsequent collection on this host was made in 1951 at a station in Dane Co. near Sauk City.

PHYLLOSTICTA sp. is present on dead, brown areas on the fronds of *Botrychium virginianum* from the New Glarus Woods, Green Co., September 8. The pycnidia are scattered, black, large, up to 200 $\mu$ diam., and the conidia are subcylindric to subfusoid, 6.5-8 x 2.5-3.5 $\mu$. Doubtfully parasitic.

PHYLLOSTICTA sp. collected on *Ulmus americana* at Alma, Buffalo Co., by Davis in August 1914, has hypophyllous pycnidia closely crowded on irregular dead brown areas which, however, appear somewhat purplish on the upper side of the leaf. The pycnidia are about 50-65 $\mu$ diam., the bacillary conidia 3-4 x 1 $\mu$. *Phyllosticta confertissima* Ell. & Ev. has conidia of the same dimensions, but they are said to be allantoid, while the pycnidia were described as amphigenous on definite, circular, dark brick-red spots 4-6 mm. diam.

PHYLLOSTICTA sp. on *Onosmodium molle* var. *occidentale* is of interest, but does not seem sufficiently well characterized to serve as a type. Green Co. near Daleyville, June 9. The scattered pycnidia, which are epiphyllous on irregular, dark brown, angled spots, are fuscous, subglobose, about 80 $\mu$ diam. Since they are almost concolorous with the spots they are most inconspicuous. Frequently the areas bearing the pycnidia are faintly zonate. The hyaline conidia are quite variable, from broadly elliptic to ovoid or subfusoid. Their approximate size range is 6-8 x 3-5 $\mu$.

PHYLLOSTICTA sp. occurred on leaves of *Echinops sphaerocephalus* (cult.) at Madison, September 8. The spots are chocolate-brown, irregular in size and shape, with numerous small, angled white areas on which the epiphyllous pycnidia are sparsely borne. The dark brown pycnidia are subglobose, about 150-165 μ diam., and the conidia are rod-shaped, 4-6 x 1.5-2 μ. I do not find any report of *Phyllosticta* on *Echinops*.

*Acer negundo* twigs, on small trees in a limited area of the University of Wisconsin Arboretum at Madison, were infected in the spring of 1951 by a conspicuous pycnidium-forming fungus which caused them to become whitened and die back to the base. The twigs are closely beset with large (500-1000 μ), applanate, shining black pycnidia which are subcuticular. The cylindric conidia are dilutely fuliginous, about 20-23 x 7-8 μ, borne on conspicuous, closely ranked phores, which line the pycnidia throughout. Perhaps an immature *Sphaeropsis*, but I have not been able to align it with any of the various species reported on *Acer negundo*, none of which have such large flat pycnidia.

PHOMA sp. on *Taphrina mirabilis* (*T. communis* according to Mix) on twigs of cultivated *Prunus* has the microscopic dimensions of *Phoma parasitica* Ell. & Ev. described (Jour. Mycol. 4:102. 1888) as on *Taphrina caerulescens*. The conidia are about 6-9 x 3 μ, but the pycnidia are gregarious and verge on pellucid, instead of being scattered and black. Coll. by Davis at Blue River, Grant Co., June 9, 1932.

CONIOTHYRIUM sp. and PHYLLOSTICTA sp. occurred on separate telia of *Puccinia anemones-virginianae* Schw. on *Anemone virginiana*, New Glarus Woods, Green Co., July 5. Under a hand lens in the field it was assumed that these were the pycnidia of *Darluca filum* which has been collected on telia of several microcyclic rusts in Wisconsin. In both cases the pycnidia are seated squarely on the telia and it seems probable they developed parasitically. Unfortunately, neither specimen is ample. The *Coniothyrium* pycnidia are subglobose, about 100 μ diam., the sooty conidia short-cylindric or sometimes ovoid, 5-6 x 3-3.5 μ. In the case of the *Phyllosticta* the fuliginous pycnidia are thin-walled, globose, about 125 μ diam., the conidia hyaline, rod-shaped, 4-7 x 1.5-2 μ.

CONIOTHYRIUM sp. on leaves of *Acer negundo* (cult.), collected by Davis at Wausau, Marathon Co., June 25, 1919, produces an effect on the host almost exactly similar to that described for *Phyllosticta pallida* Earle (Bull. Torr. Bot. Club 25:367. 1898) where the spots are "orbicular or somewhat irregular, 3-6 mm., white, arid, with a narrow, inconspicuous, yellowish-brown border." In the Wausau specimen, however, the conidia are dilute-fuliginous, oblong, about 6 x 2.5 μ, instead of 8-10 x 6-7 μ. *Coniothyrium negundinis* Tehon & Daniels is described as occurring on dead twigs.

NEOTTIOSPORA ARENARIA Syd. was reported (Farlowia 1:574. 1944) as parasitizing *Carex rostrata* in Wisconsin. J. H. Zimmerman, who is studying the Carices of the Wisconsin region has examined the specimen and finds that the host is *Carex comosa*.

ASCOCHYTA sp. occurred in small amount on grayish-brown spots on

leaves of *Prenanthes racemosa,* collected in Lafayette Co. near Platteville, August 4. The subglobose pycnidia are somewhat over 200 $\mu$ diam., succineous, and gregarious on rounded grayish-brown spots. The hyaline conidia are straight or curved, subcylindric to subfusoid, 8-16 x 3-3.5 $\mu$, mostly 10-13 x 3.5 $\mu$. An occasional conidium has two septa.

STAGONOSPORA TEPHROSIAE Greene has hitherto been seen as a relatively mild parasite on the leaflets of *Tephrosia virginiana.* In 1951, however, this organism attacked the green, developing pods with great virulence, causing their complete die-back.

STAGONOSPORA POLYTAENIAE Greene, described (Amer. Midl. Nat. 39:454. 1948) on living leaves of *Polytaenia nuttallii,* occurred in profusion on the ripening fruits of the same host, at a station near Brodhead, Green Co., August 9.

STAGONOSPORA sp. on zonate lesions on *Acerates lanuginosa* at Madison, August 27, serves to increase the confusion concerning sphaeropsidaceous forms on Asclepiadaceae in Wisconsin. The lesions are exactly those of *Stagonospora zonata* J. J. Davis, but the large spores are very different, 40-50 x 11-13 $\mu$, 8 celled, 7-septate. The individual cells are strikingly discrete.

SEPTORIA sp., which seems to have a predisposition for rust-infected leaves, occurred directly on, or associated with, lesions of *Puccinia extensicola* on *Aster pilosus* at Madison, June 15. The globose, thin-walled pycnidia, 115-130 $\mu$ diam., are closely crowded and sometimes angled by mutual compression. The pale sooty wall contrasts strongly with the prominent, thick, blackened ring of cells about the ostiole. The hyaline conidia are continuous, somewhat granular, straight or slightly curved, 20-35 x 1.5 $\mu$. The relationship between the fungi is not clear. Some of the rusted leaves did not bear the *Septoria* on the aecia, and none of those which did bore more than a single aecium per leaf. Two of the leaves had some *Septoria* spots separate from the *Septoria*-beset rust lesion, but no such spots were found on rust-free leaves, although a careful search was made. The spots are small, 2-3 mm. diam., rounded, with pale brown centers and relatively wide reddish-purple margins. In this connection it is of interest that typical *Septoria asclepiadis* Ell. & Ev. has been found centered on an abortive aecial lesion, very likely *Puccinia vexans* Farl., on *Asclepias tuberosa.*

SEPTORIA RUDBECKIAE Ell. & Halst. occurred at Madison, in August, obviously parasitic on the ray flowers of *Rudbeckia hirta.* The leaves were entirely healthy and the infection was confined to the large yellow rays, where the lesions appeared as elongate ashen streaks. Also found on the rays of *Rudbeckia subtomentosa.* In the latter case, however, the leaves were likewise infected.

SEPTORIA sp. infected the rays of *Heliopsis scabra* at Madison, in August. The small, black, amphigenous pycnidia are scattered on narrow, elongate, immarginate, brownish lesions. The slender spores are 12-25 x 1-1.5 $\mu$. It seems possible that this is a depauperate development of *Septoria silphii* Ell. & Ev. which occurs on the leaves of *Heliopsis* in Wisconsin, and which has conidia which are slender, but considerably longer than those of this specimen. However, the leaves of these particular plants were free of infection.

GLOEOSPORIUM (?) sp. occurs on *Oakesia* (*Uvularia*) *sessilifolia* collected June 19 in Dane Co. near Sauk City. The leaves are conspicuously spotted with mostly large, translucent, pale brown lesions which have a narrow darker border and are variable in shape and size, elliptic to orbicular, up to 1.5 cm. in the longest dimension. Inspection of the leaves in the field gave the impression that the spots were sterile, but sections show that a very delicate fungus is present in considerable amount. In section the colorless acervuli appear to be about 20-35 $\mu$ diam., subcuticular and hypophyllous. It is uncertain that they are isodiametric for, because of the way in which they blend with the spots, they cannot be clearly discerned, even under a fairly high-powered binocular. The rod-shaped conidia are from 5-7 x 1-1.5 $\mu$, borne on crowded phores, approx. 10 x 1.5 $\mu$.

CYLINDROSPORIUM (?) sp. infected leaves of *Polypodium virginianum* collected by Davis at Devils Lake, Sauk Co., June 1, 1922. The epiphyllous spots are prominent, 2-3 mm. diam., with cinereous centers and wide, dark purple borders. The conidiophores are very short and are arranged in a rather loose layer over the central part of the spots. The spores are slender, hyaline, continuous, curved, 25-35 x 1.5 $\mu$. Complicating the picture are small black perithecium-like bodies which are gregarious in the centers of the spots. Possibly connected with the *Cylindrosporium*.

DIDYMARIA DIDYMA (Ung.) Schroet. occurred in profusion on the leaves of *Ranunculus fascicularis* in May at a Sauk Co. station near Baraboo. There are no previous colletcions on this host in the University of Wisconsin Herbarium. Trelease, whose Wisconsin specimens are at the Missouri Botanical Garden, reported the fungus on *R. fascicularis* in Wisconsin in 1885. Very definite, rounded, straw-colored spots were produced in the current material.

RAMULARIA sp. is present on leaves of *Anaphalis margaritacea* collected by Davis at Manitou Falls, Pattison State Park, Douglas Co., August 6, 1930. The dull brown lesions are angular and elongate, involving the leaf margins. The epiphyllous, strongly fascicled conidiophores are closely gregarious, many in the tuft, hyaline, about 65-75 x 3-4 $\mu$, once or twice geniculate. They arise from a subhyaline, subglobose, stromatoid base which, while deeply sunken within the host tissue, is at the same time markedly erumpent, and from 35-50 $\mu$ diam. The conidia are hyaline, cylindric, 1-septate, 15-27 x 3.5-4.5 $\mu$. A very interesting specimen, but scarcely large enough, or sufficiently well-characterized, for use as a type. There seem to be no reports of *Ramularia* on *Anaphalis* or closely related hosts.

HELMINTHOSPORIUM sp. occurred on leaves of *Koeleria cristata* at Madison, June 15. The spots are oval, 2-3 mm. in long diam., pale tan with somewhat darker margins; conidiophores amphigenous but mostly hypophyllous, non-fasciculate, dark brown except for subhyaline tips, prominently septate, once to several times geniculate, almost straight to variously curved, 110-150 x 7-10 $\mu$; conidia stout, short-cylindric to obclavate, clear olivaceous brown, 3-8-septate, 50-110 x 16-20 $\mu$. The hilum is prominently visible and appears to be marked by a concavity in the spore wall. Some of the longer conidia are somewhat constricted at about the midpoint, tapering rather abruptly distally. Until a satisfactory monograph of *Helminthosporium* is produced,

specific determination of many forms, particularly those on graminicolous hosts, will remain uncertain and difficult.

ALTERNARIA sp. produced extensive black, sunken patches on the columnar fruiting heads of *Anemone cylindrica* at Madison in August. While probably at most only weakly parasitic, the fungus exercised a deleterious effect on the host by greatly reducing the seed set.

ALTERNARIA PANAX Whetzel caused a stem rot of small plants of *Panax quinquefolium* at Marion, Waupaca Co., in May 1911, as shown by a specimen in the Wisconsin Herbarium. Since the fungus appears to have caused damping-off, active parasitism is doubtful, but it is said to be sometimes parasitic on leaves. Two further Wisconsin specimens, from Sparta, Monroe Co., and Shiocton, Outagamie Co., are on leaves which show definite spotting, but the fungus did not fruit in either case, so far as can now be determined. Rosenbaum and Zinnsmeister (Jour. Agr. Res. 5:181. 1915) found this fungus functioning as a wound parasite on ginseng roots.

TUBERCULINA PERSICINA (Ditm.) Sacc., on the microcyclic *Puccinia physalidis* Peck on *Physalis heterophylla,* was collected at Madison in 1950. It was again collected in 1951, but in the latter specimen the phanerogamic host is *Physalis virginiana.*

*Scirpus atrovirens* in Wisconsin, and no doubt elsewhere, is very commonly infected by a fungus which produces small, sublenticular, sooty-black, perithecium-like bodies which are closely gregarious on elongate brown lesions on the living leaves. As the infection progresses the lesions become confluent and entire segments of the leaves may die back. The hypophyllous fungus is subepidermal and very inconspicuous when examined with an ordinary field hand lens. This is highly reminiscent of the sort of development that often occurs, usually late in the season, following an attack by an exogenous fungus, such as *Ramularia,* where the position of the earlier-developed tufts of conidiophores is marked by the formation of small sclerotium-like structures within the host tissue. I once overwintered infected leaves in the field, but no further development took place the following spring. Sometimes leaves that bear this organism are likewise infected with *Xenogloea eriophori* (Bres.) Syd., but I have seen nothing to indicate any connection between the two. Davis (Trans. Wis. Acad. Sci. 21:272. 1924) reported an undetermined species of *Sphaerulina* on leaves of *Scirpus atrovirens,* but the perithecia had a lower size limit of 85 $\mu$, while the upper limit noted for these bodies is 65 $\mu$.

*Brachyelytrum erectum* leaves, collected in quantity by Davis in September 1911 at a station near Phillips in Price Co., are covered with small, oval, brownish spots on which are crowded small, black, globose, epiphyllous, pycnidium-like structures, about 40-50 $\mu$ diam., which are empty so far as observed. Perhaps an early stage in the development of a species of *Mycosphaerella.* This appears to have been parasitic during the growing season.

*Cinna latifolia,* collected by Davis at Herbster, Bayfield Co., August 8, 1923, has rather large, tan, subtranslucent, oval leaf spots on which are borne pycnidia characterized by Davis in an unpublished note as follows: "Pycnidia scattered, succineous, about 100 $\mu$ broad, half as high, innate,

sporules cylindrical, mostly straight, guttulate, 17-23 x 2½ μ." A form on the borderline between *Septoria* and *Stagonospora* and perhaps somewhat immature. Many of the spores are continuous, but others have one or two septa. The pycnidia are widely scattered and are seen best by transmitted light.

*Solidago serotina* (*gigantea*) leaves, collected by Davis near Mellen, Ashland Co., July 31, 1919, have extensive dark brown, dead areas which are closely studded with large, black, innate, sclerotium-like bodies which contain a closely packed mycelium, most of the cells of which superficially resemble the so-called "Hulle" cells that occur in connection with perithecium formation in certain of the Aspergilli. That is to say, they are cells which have very heavy, thick, refractive walls, almost obliterating the cell lumen. A few days later Davis collected the same thing, at the same station, on leaves of *Aster umbellatus*. This appears to have been parasitic, but the relationships are completely unknown to me.

SCLEROTIUM sp., characterized by profuse production of aerial brown mycelium, occurs on the undersides of leaves of *Aster macrophyllus* collected by Davis near Hawkins, Rusk Co., August 26, 1918, at Cornell, Chippewa Co., September 18, 1918, and at Saxon, Iron Co., August 9, 1919. The fungus is subcuticular and appears parasitic. Interspersed among numerous small, appressed sclerotia about 30-50 μ diam. are much larger superficial sclerotia, about 0.5 mm. diam. There is a further rather scanty specimen on leaves of *Solidago patula* from Crivitz, Marinette Co., August 26, 1931.

SCLEROTIOMYCES COLCHICUS Woronichin, the name applied by Davis to a certain sclerotium-forming "honeydew" fungus has been represented in the University Herbarium by Wisconsin specimens on *Elymus virginicus, Carya cordiformis* and *Aster* sp. (Trans. Wis. Acad. Sci. 36:233. 1944), but recently discovered specimens not filed in the herbarium, but all collected by Davis in the lower Wisconsin River Valley in the summer of 1922, are on the following additional host substrates: *Onoclea sensibilis, Arisaema triphyllum, Betula nigra, Alnus incana, Quercus bicolor, Ulmus americana, U. fulva, Boehmeria cylindrica, Laportea canadensis, Clematis virginiana, Sanguinaria canadensis, Ribes cynosbati, Geranium maculatum, Ilex verticillata, Psedera vitacea, Tilia americana, Steironema ciliatum, Fraxinus pennsylvanica, Veronicastrum virginicum, Eupatorium rugosum,* and *Aster sagittifolius*. While very likely not parasitic, this fungus no doubt is, as Davis pointed out, detrimental to the plants on which it develops. It is remarkable that, on each of the diverse host plants, the fungus is strictly epiphyllous.

## ADDITIONAL HOSTS

The following hosts have not been previously recorded as bearing the fungi mentioned in Wisconsin.

SPORODINIA GRANDIS Link on *Lepiota procera*. Dane Co., Madison, August 29; also on *Amanita peckiana*, same station, August 30.

UROPHLYCTIS PLURIANNULATA (B. & C.) Farl. on *Sanicula marilandica*.

Waukesha Co., Scuppernong Prairie near Eagle, June 2. An early report of the fungus on *S. marilandica* appears dubious. The host is probably *S. gregaria*.

SPHAEROTHECA HUMILI var. FULIGINEA (Schl.) Salm. on *Gerardia pedicularia*. Dane Co. near Sauk City, September 22.

MICROSPHAERA ALNI (Wallr.) Wint. on *Lonicera canadensis*. Vilas Co., Sayner, July 21, 1936. Coll. J. J. Davis.

ERYSIPHE POLYGONI DC. on *Baptisia leucophaea*. Dane Co., Madison, September 1. Davis found *Microsphaera alni* on this host.

ERYSIPHE CICHORACEARUM DC. on *Artemisia dracunculoides*. Dane Co., Madison, October 6, 1914. Coll. J. J. Davis. The specimen was taken for the rust it bore, and the powdery mildew, which is in good maturity, was evidently overlooked. Also on *Helianthus rigidus*. Dane Co., Belleville, September 8.

MYCOSPHAERELLA THALICTRI (Ell. & Ev.) Lindau on *Thalictrum dioicum*. Dunn Co., Caryville, August 13, 1920. Coll. J. J. Davis, but not determined by him.

CLAVICEPS PURPUREA (Fr.) Tul. Sclerotia on *Glyceria grandis*. Sawyer Co., Moose River Dam, September 8, 1914. Coll. J. J. Davis. On *Elymus virginicus*. Iowa Co., Arena, September 14. On *Stipa spartea*. Dane Co., Madison, July 25. Previous to collecting ergot on it, I would have considered *Stipa* as an unlikely host. The infected seeds remain attached long after the normal ones are dropped.

PHYLLACHORA GRAMINIS (Pers.) Fckl. on *Cinna arundinacea*. Grant Co., Blue River, October 28, 1922. Coll. J. J. Davis. There are only a few mature ascomata, but these show entirely characteristic asci and spores.

ACANTHOSTIGMA OCCIDENTALE (Ell. & Ev.) Sacc. on *Antennaria fallax*. Dane Co., Madison, August 11. This specimen shows 1-celled conidia only, and therefore technically might be referred to *Pyrenochaeta* but, on the basis of past experience, I feel quite confident of the connection of the perfect and imperfect stages.

SCLEROTINIA FRUCTICOLA (Wint.) Rehm. *Monilia* stage on fruits of *Prunus pumila*. Grant Co., near Muscoda, June 22. Some of the fruits bearing the *Monilia* had been earlier infected by *Taphrina communis*.

NECTRIA CINNABARINA (Tode) Fr. on twigs of *Morus alba*. Dane Co., Madison, April 23. Although collections were not made until spring, the *Tubercularia* stage developed during the fall of 1950 on living twigs. Seemingly regularly and strongly parasitic on mulberry in the Madison region.

CHILONECTRIA CUCURBITULA (Tode) Sacc. on *Pinus strobus*. Dane Co., Madison, May 2. On trees in a plantation at the University of Wisconsin Arboretum.

PELLICULARIA FILAMENTOSA (Pat.) Rogers on *Polytrichum commune*. Dane Co., Mazomanie, August 16. I am dubious about the application of this name for the fungus concerned, and use it because it seems identical with earlier material so referred on advice of H. S. Jackson.

CHRYSOMYXA LEDI (A. & S.) DeBary I on *Picea mariana*. Vilas Co., Boulder Junction, August 12, 1936. Coll. J. J. Davis. The aecial stage seemingly has not been reported before from Wisconsin, but is recorded here with some confidence, since Davis collected leaves of *Ledum* infected with uredia of *C. ledi* at the same time, under the tree of *Picea*, and so noted on the specimens preserved.

MELAMPSORA ABIETI-CAPREARUM Tub. has been ocllected on a number of species of *Salix* in Wisconsin, but only three, *Salix discolor*, *S. longifolia* and *S. pedicellaris*, have been recorded. Others are *S. amygdaloides*, *S. balsamifera*, *S. candida*, *S. cordata*, *S. humilis*, *S. nigra*, and *S. rostrata*. The same holds true for *Melampsora bigelowii* Thum., reported on *S. amygdaloides*, *S. discolor*, *S. fragilis* × *alba*, and *S. nigra*, but with other specimens on *S. candida*, *S. cordata*, *S. glaucophylla*, *S. longifolia*, *S. petiolaris*, *S. rostrata*, and *S. alba*.

PUCCINIA EXTENSICOLA Plowr. II, III on *Carex bicknellii*. Dane Co., Madison, September 3.

UROMYCES PERIGYNIUS Halst. II on *Carex peckii*. Door Co., Fish Creek, June 28, 1919. Coll. J. J. Davis.

UROMYCES SILPHII (Burr.) Arth. I on *Aster macrophyllus*. Listed because of the report in Arthur's Manual. There is no specimen in the University of Wisconsin Herbarium.

PUCCINIA STIPAE Arth. I on *Aster oblongifolius* var. *angustatus*. Columbia Co., Black Hawk's Lookout near Prairie du Sac, June 21, 1947. In my Notes X (Amer. Midl. Nat. 39:448. 1948) this specimen was incorrectly reported as *P. extensicola* Plowr. Very characteristic and well-marked aecia of *P. stipae* have also been collected on *Aster azureus* in Green Co., Sect. 1, Town of Sylvester, May 28, 1949.

PUCCINIA ASTERIS Duby on *Aster shortii*. Green Co., New Glarus Woods, July 5.

USTILAGO LONGISSIMA var. MACROSPORA J. J. Davis (*U. davisi* Liro) on *Glyceria canadensis*. Vilas Co., Boulder Junction, July 28, 1936. Coll. J. J. Davis.

ENTYLOMA COMPOSITARUM Farl. on *Aster lateriflorus*. Dane Co., Madison, August 2.

PHYLLOSTICTA LIVIDA Ell. & Ev. on *Quercus bicolor*. Iowa Co., Arena, September 14.

PHYLLOSTICTA VIRIDIS Ell. & Kell. on *Fraxinus pennsylvanica* var. *lanceolata*. Richland Co., Lone Rock, September 24, 1936. Coll. & det. J. J. Davis. This is said to be the spermogonial state of *Mycosphaerella fraxinicola* (Schw.) House and superficially resembles *Piggotia fraxini* B. & C., the corresponding state of *Mycosphaerella effigurata* (Schw.) House. However, it appears possible to distinguish the two on the basis of the entire-walled, more deeply imbedded pycnidia, for the most part on rather definite spots in *Phyllosticta viridis*, as opposed to the imperfect, rather superficial fruiting structures which, in *Piggotia fraxini*, tend to be evenly and thickly dispersed over the entire leaf surface.

PHYLLOSTICTA MONARDAE Ell. & Barth. on *Lycopus americanus*. Dane Co., Madison, June 29. The conidia are 4-5 x 2 $\mu$.

PHYLLOSTICTA CACALIAE H. C. Greene on *Silphium terebinthinaceum*. Dane Co., Madison, August 25.

ASTEROMELLA ANDREWSII Petr. on *Gentiana clausa*. Dane Co., Madison, August 28.

ASCOCHYTA GRAMINICOLA Sacc. on *Bromus tectorum*. Waukesha Co. near Eagle, June 2. Also on *Hordeum jubatum*. Dane Co., Madison, June 17.

DARLUCA FILUM (Biv.) Cast. has been reported as parasitizing a number of species of rusts in Wisconsin, but the following rather extensive additional list has resulted from an examination of Wisconsin rust specimens in the University of Wisconsin Herbarium. Phanerogamic host names and localities and dates are omitted to conserve space. Unless noted otherwise all collections were made by J. J. Davis: *Gymnoconia peckiana* (Howe) Trott. III; *Melampsora abieti-caprearum* Tub. II; *M. euphorbiae* (Schub.) Cast. II. Coll. R. I. Evans; *Puccinia andropogonis* Schw. II; *P. argentata* (Schulz) Wint. II; *P. atrofusca* (Dudl. & Thomp.) Holw. II; *P. bardanae* Cda. II; *P. bolleyana* Sacc. II; *P. canaliculata* (Schw.) Lagh. II; *P. clintonii* Peck; *P. cnici* Mart. II; *P. ellisiana* Thum. II; *P. emaculata* Schw. II; *P. flaccida* B. & Br. II; *P. gentianae* (Str.) Link II; *P. karelica* Tranz. II, III; *P. kuhniae* Schw. II; *P. mesomajalis* B. & C.; *P. obtegens* (Lk.) Tul. II; *P. orbicula* Peck & Clint. II; *P. peridermiospora* (Ell. & Tr.) Arth. II; *P. pimpinellae* (Str.) Mart. II; *P. polygoni-amphibii* Pers. II; *P. punctata* Link II; *P. pygmaea* Erikss. II; *P. schedonnardi* Kell. & Sw. II; *P. sessilis* Schneid. II; *P. seymouriana* Arth. II; *P. violae* (Schum.) DC. II; *Uromyces acuminatus* Arth. II; *U. amphididymus* Syd. II; *U. eleocharidis* Arth. II; *U. fabae* (Pers.) Debary I; *U. halstedii* DeToni II; *U. hyperici* (Spreng.) Curt. II; *U. perigynius* Halst. II; *U. plumbarius* Peck II; *U. polygoni* (Pers.) Fckl. II; *U. proeminens* (DC.) Pass. II; *U. rudbeckiae* Arth. & Holw.

STAGONOSPORA BROMI Smith & Ramsb. on *Bromus latiglumis*. Columbia Co., Gibraltar Bluff near Okee, September 25.

STAGONOSPORA ZONATA J. J. Davis on *Asclepias verticillata*. Dane Co., Madison, June 8.

SEPTORIA NOLITANGERE Thum. on *Impatiens* sp. (cult.). Dane Co., Madison, August 31. The host is a large, coarse, purple-and-white flowered plant, seemingly not dealt with in any of the standard manuals of cultivated plants.

SEPTORIA PIMPINELLAE Ell. on immature fruits of *Polytaenia nuttallii*. Dane Co., Madison, August 17. As is characteristic of *Polytaenia*, the leaves had fallen, so it was not possible to say whether they too were infected.

SEPTORIA PHLOGIS Sacc. & Speg. on *Phlox glaberrima*. Kenosha Co., near Wis.-Ill state line on Lake Michigan shore, August 20. Microscopically identical with European specimens.

SEPTORIA ATROPURPUREA Peck on *Aster sericeus*. Grant Co., near Muscoda, June 22. Fairly characteristic in the dark spots and spores, some of

which are 70 x 2 $\mu$, or more. Also on *Aster azureus*. Lafayette Co., near Platteville, August 16. In this specimen the spores are as much as 140 x 3 $\mu$.

SELENOPHOMA DONACIS var. STOMATICOLA (Bauml.) Spr. & Johns. on *Sporobolus asper*. Vernon Co., DeSoto, September 2, 1932. Coll. J. J. Davis.

SELENOPHOMA BROMIGENA (Sacc.) Spr. & Johns. on *Bromus kalmii*. Dane Co., near Lodi. July 29.

GLOESPORIUM RUBICOLUM Ell. & Ev. on *Rubus villosus*. Rock Co., state line near Newark, July 11.

COLLETOTRICHUM GRAMINICOLA (Ces.) Wils. on *Koeleria cristata*. Sauk Co., Cactus Bluff, Town of Prairie du Sac, July 7, 1945.

PHLEOSPORA ANEMONES Ell. & Kell. on *Anemone cylindrica*. Dane Co., Rileys, July 1.

CLADOSPORIUM ASTERICOLA J. J. Davis on *Solidago graminifolia*. Dane Co., Madison, August 2.

HELMINTHOSPORIUM TURCICUM Pass. on *Zea mays*. Dane Co., Madison, September 2. Reported by me on Sudan grass, but overlooked on corn and included here for completeness' sake.

HELMINTHOSPORIUM MONOCERAS Drechsler on *Echinochloa crusgalli*. Iowa Co., Arena, September 14.

CERCOSPORA CARICIS Oud. on *Carex bicknellii*. Dane Co., Madison, August 11. This is the *C. caricina* Ell. & Dearn. of previous Wisconsin lists.

CERCOSPORA RHOINA Cooke & Ell. on *Rhus aromatica*. Dane Co., Madison, July 11.

CERCOSPORA OMPHACODES Ell. & Holw. on *Phlox glaberrima*. Kenosha Co., near Wis.-Ill. state line on Lake Michigan shore, August 20.

CERCOSPORA PENTSTEMONIS Ell. & Kell. on *Penstemon gracilis*. Dane Co., Madison, May 15.

STILBUM TOMENTOSUM Schrad. ex Fr. on *Lindbladia effusa*. Dane Co., Blue Mounds, July 19. Coll. M. P. Backus.

## ADDITIONAL SPECIES

The fungi mentioned have not been previously reported as occurring in Wisconsin.

PODOCHYTRIUM CORNUTUM F. K. Sparrow on *Stephanodiscus niagarae*. Dane Co., Madison (Lake Mendota), January 1950. Coll. H. M. Clarke. Described in Trans. Brit. Mycol. Soc. 34:170. 1951.

PERONOSPORA DAVISII C. G. Shaw on *Dracocephalum parviflorum*. Douglas Co., Gordon, July 17, 1907. Collected by J. J. Davis and first determined by him as *Peronospora lophanthi* Farl., but later referred by him to *P. hedeomae* Kell. & Sw. Shaw (Mycologia 43:445. 1951)) sets this up as a new species on the basis of the sporangia, which are much larger than those in either of the other two species.

PERONOSPORA STIGMATICOLA Raunkiaer on stigmas and anther filaments of *Mentha arvensis* var. *canadensis*. Washburn Co., Laurel P. O., August

20, 1929. Coll. W. T. McLaughlin. A very interesting find for which thanks are due to D. B. O. Savile (Mycologia 43:113. 1951) who suggested, in his note on the occurrence of this species in Canada, that other workers examine phanerogamic herbarium specimens of *Mentha* for its presence. Two other phanerogamic specimens of the same host were likewise found infected, as follows: Door Co., Jacksonport, July 20, 1938. Coll. N. C. Fassett; Sauk Co., Devils Lake, July 27, 1946. Coll. J. H. Zimmerman. Fresh material was gathered at Madison, August, 2, 1951 on the same host.

PLASMOPARA MYOSOTIDIS C. G. Shaw on *Myosotis laxa*. Iowa Co., Arena, July 20, 1922. Collected by J. J. Davis and provisionally determined by him as *Peronospora myosotidis* DeBary. Shaw (Mycologia 43:447. 1951) states that this appears to be the first record of a species of *Plasmopara* on a member of the Boraginaceae.

**Venturia sporoboli** sp. nov.

Maculis pallido-brunneis, subfusoideis, 5-7 mm. longis, interdum confluentibus; peritheciis epiphyllis, in seriebus, fulgido-nigris, subglobosis, vel globosis interdum, plerumque parvis, 60-80 x 55-65 $\mu$, pseudoparenchymaticis, setis paucis, remotiusculis, rigidis, rectis, 25-35 x 3-3.5 $\mu$, nigro-brunneis infra, apicibus pallidioribus, subacuminatis; ascis brevo-clavatis vel obovatis, 8-sporis, parvis, 25-30 x 11-13 $\mu$; ascosporis hyalinis, subcylindraceis, septis mediis, 10-13 x 3-4 $\mu$.

Spots pale brown, subfusoid in shape, about 5-7 mm. long, sometimes confluent; perithecia epiphyllous, seriate, shining black, subglobose or sometimes globose, mostly small, 60-80 x 55-65 $\mu$, pseudoparenchymatous, setae few, rather remote from the ostiole, stiff, straight, 25-35 x 3-3.5 $\mu$, blackish-brown below, slightly paler toward tip, subacuminate; asci short-clavate to obovate, 8-spored, small, 25-30 x 11-13 $\mu$; ascospores hyaline, subcylindric, septa median, 10-13 x 3-4 $\mu$.

On living leaves of *Sporobolus cryptandrus*. Columbia County, near Dekorra, Wisconsin, U. S. A., August 18, 1951.

The seriate arrangement of the perithecia seems to have resulted from adaptation to the strongly ribbed leaves. The perithecia are between the ribs. Occasionally two perithecia have become fused. The ascospores tend to be constricted at the septum and one cell is usually wider than the other. In a second collection made at the same station two weeks later an undetermined species of *Helminthosporium* occurs associated with the *Venturia*, with which, it seems possible, it may be connected. Descriptive notes of the *Helminthosporium* are as follows: Spots irregularly elongate or subfusoid, straw-colored to cinereous, 2 mm. to 1.5 cm. or even more, amphigenous; conidiophores pale brown, about 50-60 x 4-5 $\mu$, not in tufts, or at most only two or three together, basal cell noticeably enlarged and rounded, only an occasional phore geniculate, tips mostly simple with definite spore scar, straight or somewhat flexuous; conidia 50-80 x 10-13 $\mu$, 5-8 septate, medium to dark olivaceous, widest at mid-section or slightly below, rounded at both ends, but somewhat more obtuse at distal, although also more tapering, straight to moderately curved, hilum noticeable and protruding slightly beyond contour of spore.

Sprague in his recent work on the diseases of cereals and grasses in North America does not list any species of *Venturia*. *Venturia graminicola* Wint., on *Avena* in Europe, is a much larger species.

HYPOCREA CITRINA (Pers.) Fr. on *Fomes marginatus*. *Vilas Co.*, Crampton Lake,, August 12, 1910. Coll. R. A. Harper. Appearing parasitic on the current year's pore layer.

ATKINSONELLA HYPOXYLON (Peck) Diehl on *Danthonia spicata*. Marquette Co., Observatory Hill near Montello, August 6. Diehl (U. S. D .A., Agr. Monogr. 4. 1950, p. 48) created this genus to accommodate this fungus which has been variously known as *Hypocrella, Balansia, Epichloe,* and Ephelis.

STAMNARIA THUJAE Seaver on *Thuja occidentalis*. Door Co., Bailey's Harbor, October 11, 1934. Coll. J. J. Davis. Seaver (Mycologia 28:186. 1936) based this species on material sent to him from the Bailey's Harbor station. He informs me (personal communication) that he considers this species as probably parasitic.

PUCCINIA INTERVENIENS (Peck) Bethel I on *Callirhoe triangulata*. Iowa Co., near Avoca, June 22. Placed here with reservations. Morphologically the rust on *Callirhoe* perfectly matches the description in Arthur's Manual and there was no reason to doubt its identity until later in the season when what was thought to be the telial stage was collected on *Stipa spartea* at the same station. Macroscopically, the elongate telia are very similar to those of *P. interveniens* as described. Microscopically, however, the individual teliospores are very different and indeed do not well fit the specifications of those of any of the rusts known to infect *Stipa*. It is hoped to obtain further aecial material with a view to field infection tests on *Stipa spartea* at Madison where *Callirhoe* does not occur.

PYRENOCHAETA TERRESTRIS (Hansen) Gorenz, Walker & Larson causes "pink root" disease of onions (*Allium cepa*) in the commercial growing area of southeastern Wisconsin. This disease is the subject of a 1951 University of Wisconsin doctoral dissertation by E. Gasiorkiewicz.

ASCOCHYTA POLYGONICOLA Kab. & Bub. on *Polygonum arifolium*. Richland Co., Lone Rock, September 26, 1936. Coll. J. J. Davis. This corresponds closely in all respects with the description. There appears to be no previous report of a fungus on this host.

ASCOCHYTA ASCLEPIADIS Ell. & Ev. on *Asclepias sullivantii*. Dane Co., Madison, August 27. An exceptionally well-marked form, showing no sign of intergradation with *Stagonospora zonata*. It would seem that, contrary to an earlier opinion expressed by me (Amer. Midl. Nat. 44:631. 1950) this may be a good species.

STAGONOSPORA SPARTINICOLA R. Sprague on *Spartina pectinata*. Dane Co., Madison, August 13, 1949. This species (Mycologia 42:759. 1950) was described from material collected by Sprague in North Dakota and at Madison by me. The Wisconsin specimen appears parasitic.

SEPTORIA OXALIDIS Lind on *Oxalis europea*. Grant Co., Blue River, June 19, 1926. Coll. J. J. Davis. On leaves which also bear the aecia of *Puccinia sorghi*. Davis in his "Parasitic Fungi of Wisconsin" states that *Septoria*

*oxalidis* Ell. & Tracy has been reported as occurring on *Oxalis stricta* in Wisconsin. I have not been able to find a description of this species, and conclude that it is probably a nomen nudum. It seems likely that *Septoria acetosella* Dearn. & House is conspecific with *S. oxalidis* Lind.

CAMAROSPORIUM ROUMEGUERII Sacc. on *Salsola kali* var. *tenuifolia*. Grant Co., Cassville, July 5, 1920. Coll. J. J. Davis. Overrunning the leaves and stems and appearing to have been definitely parasitic.

**Gloeosporium desmodii** sp. nov.

Maculis brunneis, marginibus fusco-brunneis, subcirculis, 2-4 mm. diam.; acervulis sparsis, hypophyllis, subepidermidibus in cellis mesophyllis, parvis, 55-70 $\mu$ latis; conidiophoris brevibus, prope obsoletis; conidiis hyalinis, prope rectis vel curvis lunatis, obtusis, 20-27 x 3-4 $\mu$.

Spots brown, with a deeper brown margin, subcircular in outline, 2-4 mm. diam.; acervuli scattered, hypophyllous, subepidermal and deeply seated in the mesophyll, small, 55-70 $\mu$ wide; conidiophores short, almost obsolete; conidia hyaline, from almost straight to crescent-shaped, ends obtuse, 20-27 x 3-4 $\mu$.

On living leaves of *Desmodium canadense*. Madison, Dane County, Wisconsin, U. S. A., June 17, 1951.

None of the conidia of *G. desmodii* show even a hint of septation. It would seem that, despite their relatively great length, the fungus cannot be properly assigned to *Cylindrosporium*. Very similar spots have been noted on the leaves of this host on other occasions, but hitherto have always proved sterile.

**Gloeosporium ceanothi** sp. nov.

Maculis brunneis, irregularibus, angulosis, saepe confluentibus; acervulis numerosis, amphigenis, epiphyllis plerumque, 30-100 $\mu$ diam. ca., variis, confluentibus interdum; conidiophoris hyalinis, confertis, brevibus, cylindraceis, 5-6 x 3 $\mu$; conidiis hyalinis, ellipsoideis vel subcylindraceis vel subfusoideis, 10-16 x 3.5-5.5 $\mu$.

Spots brown, irregular, angled, often confluent; acervuli numerous, amphigenous, mostly epiphyllous, approx. 30-100 $\mu$ diam., variable, sometimes confluent; conidiophores hyaline, crowded, short, cylindric, about 5-6 x 3 $\mu$; conidia hyaline, ellipsoid, subcylindric or subfusoid, 10-16 x 3.5-5.5 $\mu$.

On living leaves of *Ceanothus americanus*. Madison, Dane County, Wisconsin, U. S. A., June 11, 1951.

The host leaves show a very strong "curl" and the parasite is highly destructive. Conidia are formed in profusion and are pink in mass. In late August the fungus was noted to have caused destruction of the immature fruits, which had become blackened and mummified and bore numerous acervuli.

The species here described as *Gloeosporium corni* is on the borderline between *Gloeosporium* and *Colletotrichum*. An occasional acervulus bears a seta or two, although most are without setae, and the large, more or less oblong, conidia are not of the type usually found in fungi described as species of *Colletotrichum*. The few setae observed were clear brown (somewhat paler at tip), slender, acuminate, 50-65 x 3.5-4 $\mu$, 2-3 septate.

**Gloeosporium corni** sp. nov.

Maculis obscuro-brunneis, marginibus angustis, atropurpureis, irregularibus, linearibus, fusoideis, vel orbicularibus, 4 mm.-1.5 cm.; acervulis epiphyllis, saepe nervisequentibus, confluentibus interdum, 65-115 μ diam.; conidiophoris tenuibus, confertis, 10-12 x 2.5-3 μ; conidiis hyalinis, subcylindraceis vel subfusoideis, magnis, 12-20 x 4-7 μ.

Spots dull brown, with narrow, dark purple margin, irregular, linear, fusoid, or orbicular, 4 mm.-1.5 cm.; acervuli epiphyllous, often nervisequous, sometimes confluent, 65-115 μ diam.; conidiophores slender, crowded, 10-12 x 2.5-3 μ; condia hyaline, subcylindric or subfusoid, large, 12-20 x 4-7 μ.

On living leaves of gray dogwood, *Cornus femina* Mill. Madison, Dane County, Wisconsin, U. S. A., August 2, 1951.

In mass the conidia are bright pink and show up prominently against the dull spots. Seymour lists no species of *Gloeosporium* or *Colletotrichum* on any species of *Cornus*.

**Gloeosporium pentstemonicola** sp. nov.

Maculis lato-fusoideis vel suborbicularibus, pallido-brunneis, marginibus angustis, purpureis, 0.5-1 cm. ca.; acervulis amphigenis, plerumque epiphyllis, brunneis, gregariis vel confertis, circulis vel subellipsoideis, 100-200 μ diam. ca.; conidiophoris tenuibus, brevibus, confertis; conidiis hyalinis, subfusoideis vel lunatis, 11-16 x 3.5-4.5 μ.

Spots broadly fusoid to suborbicular, pale brown with narrow purple margins, approx. 0.5-1 cm. diam.; acervuli amphigenous, mostly epiphyllous, brownish, gregarious to crowded, rounded or subellipsoid, approx. 100-200 μ diam.; conidiophores slender, short, crowded; conidia hyaline, subfusoid to lunate, 11-16 x 3.5-4.5 μ.

On the overwintered, but still green, lower leaves of *Pentstemon hirsutus*. Madison, Dane County, Wisconsin, U. S. A., May 15, 1951. A rather similar, but evidently not identical, fungus was collected in April 1949 at the same station in small amount on the overwintered basal leaves of *Pentstemon grandiflorus* (Amer. Midl. Nat. 44:632. 1950).

RAMULARIA MACROSPORA Fres. on *Campanula rotundifolia*. Waukesha Co., near Eagle, June 2. Also collected, in greater quantity, near Klevenville, Dane Co., July 1.

**Cladosporium trichophilum** sp. nov.

Maculis inconspicuis, angulosis, parvis, 1-3 mm. diam., pallido-brunneis infra, sordido-brunneis supra; hyphis claro- vel pallido-brunneis, hypophyllis, effusis, in pilis; conidiophoris variis, brevibus plerumque, ca. 25-60 x 4.5-7 μ, 1-2-septatis, saepe 1-geniculatis, subdenticulatis; conidiis pallido-fuligineis, levibus, subfusoideis vel obclavatis, 1-septatis, 19-27 v 4-6 μ.

Spots inconspicuous, angled, small, 1-3 mm. diam., tan below, sordid brown above; hyphae clear- to pale-brown, hypophyllous, effuse, covering trichomes; conidiophores variable, mostly short, about 25-60 x 4.5-7 μ, 1-2-septate, often once-geniculate, subdenticulate; conidia dilute-fuliginous, smooth, subfusoid or obclavate, 1-septate, 19-27 x 4-6 μ.

On living leaves of *Lonicera hirsuta*. Hawkins, Rusk County, Wisconsin, U. S. A., August 26, 1918 Coll. J. J. Davis.

Davis tentatively identified this as a *Cercospora*, but never described it, or mentioned it in any of his notes. A specimen was sent to Chupp who regards it as definitely not belonging in *Cercospora*. The outstanding characteristic of the fungus is the strong tendency of the hyphae to ascend the host trichomes and to become aggregated in spore-bearing wefts at the trichome tips. The hyphae become compressed into rope-like strands from which the conidiophores project at right angles. At the apices of the trichomes the strands are clumped in a more or less amorphous mass, a prominent feature when the lesions are examined under a binocular at medium magnification. The production of conidia is acropleurogenous and there are pronounced spore scars on both phores and conidia. There is no evidence of catenulation. Thanks to the hairy surface of the host and the complexly interwoven hyphae, a great many conidia were trapped, and are thus still available for examination more than thirty years after collection.

**Cladosporium artemisiae** sp. nov.

Maculis nullis, fasciis sparsis, epiphyllis; conidiophoris paucis in fasciis, divergentibus, fuscis, apicibus pallidioribus, geniculatis, 20-60 x 4-5 $\mu$, 2-4-septatis; conidiis subcylindraceis vel subfusoideis, olivaceo-griseis, 1-septatis, 16-26 x 3.5-5 $\mu$.

Spots none, tufts scattered, epiphyllous; conidiophores few in the tufts, spreading, dark brown with paler tips, geniculate, 20-60 x 4-5 $\mu$, 2-4-septate; conidia subcylindric or subfusoid, olivaceous gray, 1-septate, 16-26 x 3.5-5 $\mu$.

On living leaves of *Artemisia caudata*. Madison, Dane County, Wisconsin, U. S. A., July 7, 1951.

A very inconspicuous species, discovered when inspecting aged and discolored lower stem leaves. Further examination showed that the fully green upper leaves were likewise infected. An occasional conidium shows two septa.

HELMINTHOSPORIUM TRISEPTATUM Drechsler on *Agrostis alba*. Dane Co., Madison, August 11. Notable for, and easily distinguished by, the wing-like thickenings on the upper portions of the conidiophore walls.

CERCOSPORA HYPERICI Tehon & Daniels on *Hypericum sphaerocarpum*. Green Co., near Albany, July 24. A small, delicate species. The conidia in my specimen are as described (Mycologia 19:127. 1927), except that a few are somewhat longer, as are the conidiophores which also show a degree of geniculation, perhaps the result of greater maturity in the Wisconsin material.

CERCOSPORIA KALMIAE Ell. & Ev. on *Andromeda glaucophylla*. Jefferson Co., Hope Lake Bog near the village of London, June 24. 1950. Coll. E. A. Stowell. Very few conidia were found, but the material seems sufficiently similar to specimens on *Kalmia* to warrant a record.

CERCOSPORA ECHII Wint. on *Echium vulgare*. Dane Co., near Klevenville, July 1.

STEMPHYLIUM CUCURBITACEARUM Osner on *Echinocystis lobata*. Grant Co., Millville, September 22, 1913. Coll. J. J. Davis. Osner (Jour. Agr. Res. 13:299. 1918) based this species on collections made on leaves of cucumbers in Indiana and Ohio in 1915 and 1916. The specimen on *Echinocystis* fits both description and illustrations very closely. It would be of interest to know whether this fungus is indigenous, or whether the *Echinocystis* was infected from adjacent cultivated cucurbits.

# A Phenological Study of the Flora of the Chicago Region

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This survey represents the results of data taken on 296 field trips in the Chicago area during the nine-year period from 1942 to 1950 inclusive. For the purpose of this paper, the Chicago area includes the counties of Walworth and Kenosha in Wisconsin; Lake, McHenry, Kane, Du Page, Cook, Will, and Kankakee in Illinois; Lake, Porter, and La Porte in Indiana; and Berrien in Michigan.

No attempt has been made to determine average blooming dates, but rather the very earliest and latest recorded for each species at any time during the nine-year survey period. None of the records were made from cultivated plants, but always from wild specimens in the field. Undoubtedly most of the dates cited will eventually be extended by future workers, especially during years having a very early spring or very late autumn.

Data has been omitted concerning the more inconspicuous flowers; such as grasses, sedges, rushes, and catkin-bearing trees and shrubs. Also those species have been omitted which, due to their rarity, have been observed only a few times. Scientific nomenclature is in accord with *Gray's Manual of Botany* (eighth edition).

It is a frequent phenomenon for some early blooming species to bloom again in the autumn, skipping a good portion of the summer. In such cases the normal flowering dates are given, and the fact of a possible recurrent autumnal blooming period is indicated by an asterisk after the latest date shown.

Recognized varieties and forms have been included with the species, as they usually do not seem to differ phenologically from the type.

| Scientific Name | Common Name | Earliest Date | Latest Date |
|---|---|---|---|
| Abutilon theophrasti | Indian mallow | Jul. 19 | Oct. 8 |
| Acalypha rhomboidea | mercury | Jun. 22 | Oct. 8 |
| Achillea millefolium | yarrow | May 25 | Nov. 5 |
| Actaea pachypoda | white baneberry | May 9 | Jun. 3 |
| Agastache nepetoides | giant hyssop | Jul. 19 | Aug. 26 |
| Agrimonia gryposepala | agrimony | Jul. 4 | Sep. 26 |
| Aletris farinosa | colic root | Jun. 22 | Jul. 25 |
| Alisma subcordatum | water plantain | Jul. 9 | Sep. 6 |
| Allium canadense | wild garlic | Jun. 13 | Jul. 3 |
| Allium cernuum | nodding wild onion | Jun. 29 | Sep. 11 |
| Allium tricoccum | wild leek | Jun. 26 | Aug. 6 |

| Scientific Name | Common Name | Earliest Date | Latest Date |
|---|---|---|---|
| Amaranthus albus | tumbleweed | Jul. 28 | Sep. 12 |
| Amaranthus graecizans | creeping amaranth | Jul. 2 | Oct. 8 |
| Amaranthus retroflexus | pigweed | Jul. 29 | Oct. 1 |
| Ambrosia artemisiifolia elatior | short ragweed | Aug. 9 | Sep. 23 |
| Ambrosia trifida | giant ragweed | Jul. 31 | Sep. 8 |
| Amelanchier arborea | Juneberry | Apr. 22 | May 20 |
| Amorpha canescens | lead plant | Jun. 29 | Jul. 19 |
| Amphicarpa bracteata | hog peanut | Aug. 22 | Sep. 14 |
| Anemone canadensis | prairie anemone | May 27 | Aug. 12 |
| Anemone cylindrica | thimbleweed | Jun. 14 | Aug. 9 |
| Anemone quinquefolia interior | wood anemone | Apr. 1 | May 30 |
| Anemone virginiana | tall anemone | Jun. 10 | Aug. 16 |
| Anemonella thalictroides | rue anemone | Mar. 28 | Jun. 13 |
| Angelica atropurpurea | great angelica | May 20 | Jun. 19 |
| Antennaria plantaginifolia | pussy toes | Apr. 7 | Jun. 13 |
| Anthemis cotula | dog fennel | Jun. 22 | Oct. 10 |
| Apios americana | ground nut | Aug. 6 | Sep. 6 |
| Apocynum androsaemifolium | spreading dogbane | Jun. 19 | Aug. 30 |
| Apocynum cannabinum | Indian hemp | Jun. 7 | Sep. 5 |
| Aquilegia canadensis | wild columbine | Apr. 15 | Jul. 5 |
| Arabis canadensis | sickle pod | May 23 | Jul. 12 |
| Arabis laevigata | smooth bank cress | Apr. 28 | Aug. 7 |
| Arabis lyrata | sand cress | Apr. 7 | Sep. 25 |
| Arabis perstellata shortii | toothed cress | Apr. 17 | Jun. 21 |
| Aralia nudicaulis | wild sarsaparilla | May 9 | Jul. 12 |
| Arctium minus | burdock | Jul. 25 | Sep. 28 |
| Arctostaphylos uva-ursi coactilis | bearberry | Apr. 7 | Jun. 8 |
| Arenaria lateriflora | wood sandwort | Apr. 27 | Jul. 3 |
| Arenaria serpyllifolia | thyme-leaved sandwort | May 21 | Jul. 15 |
| Arenaria stricta | stiff sandwort | May 26 | Jul. 12 |
| Arisaema atrorubens | Jack-in-the-pulpit | Apr. 15 | Jul. 15 |
| Arisaema dracontium | green dragon | May 11 | Jun. 27 |
| Artemisia caudata | tall wormwood | Aug. 11 | Oct. 27 |
| Asarum canadense | wild ginger | Apr. 8 | Jun. 26 |
| Asclepias incarnata | swamp milkweed | Jul. 8 | Aug. 28 |
| Asclepias sullivantii | prairie milkweed | Jun. 30 | Jul. 31 |
| Asclepias syriaca | common milkweed | Jun. 25 | Aug. 30 |
| Asclepias tuberosa | butterfly weed | Jun. 22 | Sep. 8 |
| Asclepias verticillata | whorled milkweed | Jul. 2 | Sep. 12 |
| Asimina triloba | papaw | May 4 | May 30 |
| Asparagus officinalis | asparagus | May 12 | Sep. 16 |
| Aster azureus | sky-blue aster | Aug. 25 | Nov. 5 |
| Aster dumosus | rice button aster | Aug. 19 | Oct. 22 |
| Aster ericoides | small white aster | Aug. 16 | Oct. 1 |
| Aster lateriflorus | side-flowering aster | Jul. 29 | Oct. 10 |
| Aster linariifolius | stiff aster | Aug. 20 | Oct. 27 |
| Aster macrophyllus | great-leaved aster | Aug. 6 | Oct. 9 |
| Aster novae-angliae | New England aster | Jul. 28 | Oct. 27 |
| Aster pilosus | white heath aster | Aug. 22 | Nov. 17 |
| Aster ptarmicoides | sand aster | Aug. 6 | Oct. 1 |
| Aster sagittifolius | arrow-leaved aster | Aug. 24 | Nov. 17 |
| Aster simplex | Michaelmas daisy | Jul. 26 | Nov. 2 |
| Aster umbellatus | flat-top aster | Aug. 9 | Oct. 6 |
| Baptisia leucantha | white wild indigo | Jun. 7 | Jul. 26 |
| Baptisia leucophaea | cream wild indigo | May 16 | Jun. 14 |

| Scientific Name | Common Name | Earliest Date | Latest Date |
|---|---|---|---|
| Barbarea vulgaris | winter cress | Apr. 17 | Jul. 15 |
| Berteroa incana | hoary alyssum | Jun. 15 | Aug. 25 |
| Bidens coronata | swamp marigold | Jul. 3 | Sep. 28 |
| Bidens frondosa | beggar's ticks | Aug. 16 | Oct. 13 |
| Boehmeria cylindrica | false nettle | Jul. 24 | Sep. 2 |
| Brassica nigra | black mustard | May 12 | Oct. 13 |
| Cacalia atriplicifolia | pale Indian plantain | Aug. 1 | Sep. 22 |
| Cacalia tuberosa | prairie Indian plantain | Jun. 9 | Aug. 8 |
| Cakile edentula lacustris | sea rocket | Jul. 1 | Oct. 6 |
| Calopogon pulchellus | grass pink | Jun. 20 | Aug. 9 |
| Caltha palustris | marsh marigold | Mar. 30 | Jun. 10 |
| Camassia scilloides | wild hyacinth | May 19 | Jun. 10 |
| Campanula americana | tall bellflower | Jul. 19 | Nov. 3 |
| Campanula aparinoides | marsh bellflower | Jul. 12 | Sep. 19 |
| Campanula rotundifolia | harebell | Jun. 3 | Sep. 19 |
| Capsella bursa-pastoris | shepherd's purse | Apr. 1 | Oct. 31 |
| Cardamine bulbosa | bulbous cress | Apr. 15 | Jun. 21 |
| Cardamine douglassii | purple spring cress | Mar. 28 | May 18 |
| Cassia fasciculata | partridge pea | Jul. 24 | Oct. 9 |
| Castilleja coccinea | Indian paintbrush | May 17 | Sep. 8 |
| Caulophyllum thalictroides | blue cohosh | Apr. 15 | May 7 |
| Ceanothus americanus | New Jersey tea | Jun. 30 | Sep. 5 |
| Celastrus scandens | climbing bittersweet | May 24 | Jun. 21 |
| Centaurium pulchellum | centaury | Jul. 17 | Oct. 1 |
| Cephalanthus occidentalis | buttonbush | Jul. 4 | Aug. 30 |
| Cerastium vulgatum | mouse-ear chickweed | Mar. 30 | Nov. 17 |
| Chaenorrhinum minus | small snapdragon | Jun. 11 | Sep. 28 |
| Chaerophyllum procumbens | wild chervil | Apr. 28 | May 30 |
| Chelone glabra | turtlehead | Aug. 20 | Sep. 19 |
| Chenopodium album | lamb's quarters | Jun. 25 | Oct. 13 |
| Chrysanthemum leucanthemum pinnatifidum | common white daisy | May 19 | Nov. 3 |
| Cichorium intybus | chicory | Jun. 13 | Oct. 10 |
| Cicuta maculata | water hemlock | Jun. 22 | Oct. 9 |
| Circaea quadrisulcata canadensis | enchanter's nightshade | Jul. 4 | Aug. 9 |
| Cirsium arvense | Canada thistle | Jun. 13 | Oct. 8 |
| Cirsium discolor | field thistle | Aug. 2 | Oct. 14 |
| Cirsium muticum | swamp thistle | Aug. 16 | Oct. 20 |
| Cirsium vulgare | bull thistle | Jul. 25 | Nov. 3 |
| Claytonia virginica | spring beauty | Mar. 25 | Jun. 14 |
| Comandra richardsiana | false toadflax | Apr. 22 | Jul. 3 |
| Commelina communis | day flower | Jun. 19 | Oct. 8 |
| Convolvulus arvensis | field bindweed | Jun. 14 | Sep. 11 |
| Convolvulus sepium | hedge bindweed | Jun. 6 | Sep. 28 |
| Coreopsis lanceolata | sand coreopsis | May 26 | Jul. 25 |
| Coreopsis palmata | prairie coreopsis | Jun. 29 | Jul. 26 |
| Coreopsis tripteris | tall coreopsis | Aug. 6 | Sep. 25 |
| Cornus florida | flowering dogwood | May 2 | Jun. 3 |
| Cornus racemosa | gray dogwood | May 30 | Jul. 1 |
| Cornus stolonifera | red-osier dogwood | May 4 | Sep. 25 |
| Crataegus mollis | red haw | Apr. 17 | May 30 |
| Crataegus punctata | dotted haw | Apr. 28 | Jun. 17 |
| Cryptotaenia canadensis | honewort | May 28 | Sep. 6 |
| Cuscuta gronovii | common dodder | Jul. 25 | Sep. 11 |
| Cycloloma atriplicifolium | winged pigweed | Jul. 25 | Sep. 28 |

| Scientific Name | Common Name | Earliest Date | Latest Date |
|---|---|---|---|
| Cynoglossum officinale | hound's tongue | May 22 | Jun. 22 |
| Cypripedium calceolus (vars. parviflorum and pubescens) | yellow lady's slipper | May 18 | Jun. 13 |
| Daucus carota | wild carrot | Jun. 26 | Nov. 3 |
| Dentaria laciniata | toothwort | Apr. 13 | May 16 |
| Desmodium canadense | showy tick clover | Jul. 2 | Sep. 16 |
| Dicentra canadensis | squirrel corn | Apr. 24 | May 30 |
| Dicentra cucullaria | Dutchman's breeches | Mar. 31 | May 10 |
| Diervilla lonicera | bush honeysuckle | Jun. 4 | Aug. 22 |
| Dodecatheon meadia | shooting star | May 5 | Jun. 15 |
| Drosera rotundifolia | round-leaved sundew | Jun. 30 | Aug. 22 |
| Echinacea pallida | purple coneflower | Jun. 29 | Jul. 4 |
| Echinocystis lobata | wild cucumber | Aug. 1 | Sep. 13 |
| Ellisia nyctelea | ellisia | Apr. 28 | Jun. 6 |
| Epilobium coloratum | willow herb | Jul. 5 | Sep. 2 |
| Erechtites hieracifolia | fireweed | Aug. 9 | Oct. 6 |
| Erigeron annuus | daisy fleabane | May 9 | Nov. 3 |
| Erigeron canadensis | horseweed | Jul. 17 | Oct. 20 |
| Erigeron philadelphicus | marsh fleabane | May 14 | Jul. 19 |
| Erigeron pulchellus | robin's plantain | May 4 | Jun. 19 |
| Erigeron strigosus | daisy fleabane | May 3 | Oct. 31 |
| Eryngium yuccifolium | rattlesnake master | Jul. 2 | Sep. 6 |
| Erythronium albidum | white adder's tongue | Mar. 30 | May 13 |
| Erythronium americanum | yellow adder's tongue | Apr. 13 | May 10 |
| Euonymus obovatus | running strawberry bush | May 11 | Jun. 21 |
| Eupatorium altissimum | tall boneset | Aug. 9 | Sep. 28 |
| Eupatorium maculatum | Joe Pye weed | Jul. 21 | Sep. 25 |
| Eupatorium perfoliatum | boneset | Jul. 28 | Oct. 1 |
| Eupatorium rugosum | white snakeroot | Jul. 19 | Oct. 9 |
| Eupatorium serotinum | late boneset | Aug. 24 | Oct. 3 |
| Euphorbia corollata | flowering spurge | May 10 | Oct. 6 |
| Euphorbia cyparissias | cypress spurge | May 17 | Aug. 25 |
| Euphorbia dentata | toothed spurge | Jul. 25 | Sep. 16 |
| Euphorbia maculata | nodding spurge | Jul. 3 | Sep. 28 |
| Euphorbia polygonifolia | sand spurge | Jul. 9 | Nov. 5 |
| Euphorbia supina | spotted spurge | Jun. 25 | Sep. 22 |
| Floerkea proserpinacoides | false mermaid | Apr. 24 | May 30 |
| Fragaria virginiana | wild strawberry | Apr. 7 | *Jun. 21 |
| Galinsoga ciliata | quickweed | Jun. 17 | Oct. 8 |
| Galium aparine | goose grass | Apr. 15 | Jun. 15 |
| Galium boreale | Northern bedstraw | Jun. 10 | Sep. 6 |
| Galium concinnum | shining bedstraw | May 8 | Jul. 26 |
| Galium obtusum | wild madder | Jun. 5 | Aug. 9 |
| Galium tinctorium | marsh bedstraw | Jun. 26 | Sep. 1 |
| Galium triflorum | sweet-scented bedstraw | Jun. 3 | Aug. 24 |
| Gaura biennis | biennial gaura | Jul. 31 | Oct. 10 |
| Gaylussacia baccata | huckleberry | Apr. 22 | Jun. 15 |
| Gentiana andrewsii | closed gentian | Sep. 7 | Oct. 20 |
| Gentiana crinita | fringed gentian | Sep. 12 | Nov. 5 |
| Geranium maculatum | wild geranium | Apr. 8 | Jul. 4 |
| Gerardia pedicularia ambigens | clammy false foxglove | Jul. 19 | Aug. 30 |
| Gerardia purpurea | purple gerardia | Aug. 15 | Oct. 13 |
| Gerardia tenuifolia | slender gerardia | Aug. 8 | Sep. 12 |
| Geum canadense | wood avens | Jun. 13 | Aug. 16 |
| Geum laciniatum trichocarpum | rough avens | Jun. 6 | Jul. 12 |

| Scientific Name | Common Name | Earliest Date | Latest Date |
|---|---|---|---|
| Glechoma hederacea | ground ivy | Apr. 6 | Jun. 19 |
| Gnaphalium obtusifolium | old-field balsam | Aug. 8 | Oct. 9 |
| Gratiola neglecta | hedge hyssop | May 25 | Sep. 11 |
| Hackelia virginiana | stickseed | Jul. 9 | Aug. 24 |
| Hamamelis virginiana | witch hazel | Sep. 2 | Dec. 27 |
| Helenium autumnale | sneezeweed | Jul. 25 | Nov. 3 |
| Helianthemum canadense | rockrose | May 23 | Jul. 12 |
| Helianthus annuus | annual sunflower | Jul. 12 | Sep. 28 |
| Helianthus decapetalus | pale sunflower | Jul. 19 | Oct. 14 |
| Helianthus divaricatus | woodland sunflower | Jul. 14 | Oct. 6 |
| Helianthus grosseserratus | prairie sunflower | Jul. 4 | Oct. 10 |
| Helianthus laetiflorus rigidus | rough sunflower | Jul. 2 | Oct. 8 |
| Helianthus occidentalis | Western sunflower | Aug. 6 | Sep. 19 |
| Helianthus petiolaris | petioled sunflower | Jun. 11 | Oct. 22 |
| Heliopsis helianthoides | false sunflower | Jul. 2 | Sep. 5 |
| Hepatica acutiloba | hepatica | Mar. 28 | May 10 |
| Hepatica americana | hepatica | Mar. 25 | May 7 |
| Heracleum maximum | cow parsnip | May 20 | Jul. 3 |
| Heuchera richardsonii grayana | alum root | May 19 | Jul. 4 |
| Hibiscus trionum | modesty | Aug. 4 | Oct. 14 |
| Hieracium canadense fasciculatum | Canada hawkweed | Aug. 20 | Oct. 20 |
| Hieracium gronovii | hairy hawkweed | Jul. 15 | Aug. 30 |
| Houstonia caerulea | bluets | Apr. 27 | Aug. 22 |
| Hydrophyllum appendiculatum | great waterleaf | May 14 | Jun. 26 |
| Hydrophyllum virginianum | Virginia waterleaf | May 11 | Jun. 17 |
| Hypericum kalmianum | Kalm's St. John's wort | Jun. 30 | Sep. 1 |
| Hypericum perforatum | common St. John's wort | Jun. 26 | Aug. 24 |
| Hypericum virginicum | marsh St. John's wort | Jul. 25 | Aug. 24 |
| Hypoxis hirsuta | yellow star grass | Apr. 27 | Jul. 3 |
| Impatiens capensis | spotted touch-me-not | Jul. 5 | Sep. 26 |
| Iris virginica shrevei | blue flag | May 23 | Jul. 4 |
| Isopyrum biternatum | false rue anemone | Apr. 1 | May 30 |
| Kochia scoparia | burning bush | Aug. 6 | Oct. 8 |
| Krigia biflora | false dandelion | May 18 | Jul. 4 |
| Krigia virginica | dwarf dandelion | May 4 | Aug. 6 |
| Lactuca canadensis | wild lettuce | Jun. 22 | Sep. 12 |
| Lactuca scariola | prickly lettuce | Jul. 28 | Nov. 3 |
| Laportea canadensis | wood nettle | Jul. 4 | Sep. 26 |
| Lappula echinata | beggar's lice | May 18 | Aug. 24 |
| Lathyrus palustris | marsh vetchling | Jun. 5 | Sep. 14 |
| Lathyrus venosus | showy vetchling | Jun. 6 | Jun. 25 |
| Leonurus cardiaca | motherwort | Jun. 13 | Sep. 26 |
| Lepidium campestre | field cress | Apr. 22 | Jun. 30 |
| Lepidium densiflorum | peppergrass | Apr. 22 | Oct. 11 |
| Lepidium virginicum | peppergrass | May 6 | Dec. 8 |
| Lespedeza capitata | bush clover | Aug. 15 | Sep. 8 |
| Lespedeza hirta | bush clover | Aug. 19 | Sep. 6 |
| Liatris aspera | blazing star | Jul. 17 | Nov. 5 |
| Liatris cylindracea | blazing star | Jul. 17 | Sep. 14 |
| Liatris pycnostachya | blazing star | Jul. 25 | Sep. 6 |
| Liatris spicata | blazing star | Jul. 25 | Sep. 28 |
| Lilium michiganense | Turk's cap lily | Jul. 2 | Jul. 26 |
| Lilium philadelphicum andinum | meadow lily | Jun. 11 | Jul. 9 |
| Linaria canadensis | blue toadflax | Apr. 22 | Jun. 21 |
| Linaria vulgaris | butter-and-eggs | Jun. 15 | Oct. 22 |

| Scientific Name | Common Name | Earliest Date | Latest Date |
|---|---|---|---|
| Lindera benzoin | spicebush | Apr. 7 | May 7 |
| Linum medium texanum | yellow flax | Jul. 1 | Oct. 1 |
| Lippia lanceolata recognita | fog fruit | Jul. 9 | Sep. 22 |
| Liriodendron tulipifera | tulip tree | Jun. 4 | Jul. 12 |
| Lithospermum canescens | hoary puccoon | Apr. 20 | Jul. 26 |
| Lithospermum croceum | hairy puccoon | Apr. 22 | Sep. 11 |
| Lithospermum incisum | fringed puccoon | May 8 | Jun. 8 |
| Lobelia cardinalis | cardinal flower | Aug. 1 | Sep. 16 |
| Lobelia inflata | Indian tobacco | Aug. 6 | Aug. 30 |
| Lobelia kalmii | brook lobelia | Jul. 31 | Oct. 13 |
| Lobelia siphilitica | great blue lobelia | Jul. 28 | Oct. 9 |
| Lobelia spicata | pale spiked lobelia | Jun. 2 | Aug. 25 |
| Lonicera dioica | red honeysuckle | May 4 | Jun. 27 |
| Lonicera tatarica | Tartarian honeysuckle | Apr. 28 | Jun. 8 |
| Ludwigia alternifolia | seedbox | Jul. 14 | Aug. 24 |
| Lupinus perennis | wild lupine | May 4 | Jun. 22 |
| Lychnis alba | white campion | May 12 | Oct. 8 |
| Lycopus americanus | water horehound | Jul. 24 | Sep. 23 |
| Lycopus virginicus | bugle weed | Aug. 7 | Sep. 22 |
| Lysimachia ciliata | fringed loosestrife | Jun. 18 | Aug. 9 |
| Lysimachia nummularia | moneywort | Jun. 17 | Jul. 28 |
| Lysimachia quadriflora | marsh loosestrife | Jun. 28 | Aug. 25 |
| Lysimachia terrestris | swamp candles | Jun. 22 | Jul. 26 |
| Lysimachia thyrsiflora | swamp loosestrife | May 26 | Jun. 21 |
| Lythrum alatum | winged loosestrife | Jun. 22 | Sep. 11 |
| Maianthemum canadense | false lily-of-the-valley | May 6 | Jun. 21 |
| Malva neglecta | cheeses | Jun. 14 | Sep. 16 |
| Matricaria matricarioides | pineapple weed | May 25 | Jul. 26 |
| Medeola virginiana | Indian cucumber root | May 18 | Jun. 21 |
| Medicago lupulina | black medick | May 5 | Oct. 13 |
| Medicago sativa | alfalfa | Jun. 9 | Oct. 8 |
| Melilotus alba | white sweet clover | Jun. 3 | Nov. 5 |
| Melilotus officinalis | yellow sweet clover | May 27 | Oct. 14 |
| Mentha arvensis | wild mint | Jul. 19 | Sep. 25 |
| Mertensia virginica | bluebells | Mar. 31 | May 20 |
| Mimulus ringens | monkey flower | Jul. 19 | Sep. 8 |
| Mirabilis nyctaginea | wild four o'clock | May 27 | Aug. 11 |
| Mitella diphylla | bishop's cap | Apr. 15 | Jun. 21 |
| Mollugo verticillata | carpet weed | Jun. 19 | Oct. 8 |
| Monarda fistulosa | wild bergamot | Jun. 29 | Oct. 9 |
| Monarda punctata villicaulis | horse mint | Jul. 9 | Sep. 22 |
| Myosotis scorpioides | forget-me-not | May 22 | Sep. 17 |
| Myosotis verna | white forget-me-not | May 3 | Jun. 15 |
| Nasturtium officinale | water cress | Apr. 22 | Jun. 29 |
| Nepeta cataria | catnip | Jun. 22 | Sep. 26 |
| Nuphar advena | yellow pond lily | May 18 | Sep. 14 |
| Nymphaea tuberosa | white water lily | Jun. 8 | Sep. 19 |
| Oenothera biennis | evening primrose | Jun. 20 | Nov. 3 |
| Oenothera rhombipetala | sand primrose | Jun. 20 | Oct. 27 |
| Opuntia humifusa | prickly pear cactus | Jun. 27 | Jul. 25 |
| Osmorhiza claytoni | hairy sweet cicely | May 3 | Jun. 13 |
| Osmorhiza longistylis | smooth sweet cicely | May 3 | Jun. 27 |
| Oxalis europaea | yellow wood sorrel | May 25 | Oct. 13 |
| Oxalis stricta | yellow wood sorrel | May 6 | Oct. 30 |
| Oxalis violacea | violet wood sorrel | Apr. 3 | Jun. 8 |

| Scientific Name | Common Name | Earliest Date | Latest Date |
|---|---|---|---|
| Oxypolis rigidior | cowbane | Aug. 6 | Sep. 17 |
| Panax trifolius | dwarf ginseng | Apr. 15 | May 30 |
| Parietaria pensylvanica | pellitory | May 16 | Jul. 31 |
| Parnassia glauca | grass of Parnassus | Sep. 6 | Oct. 1 |
| Parthenium integrifolium | wild quinine | Jun. 14 | Sep. 6 |
| Pastinaca sativa | wild parsnip | May 26 | Sep. 28 |
| Pedicularis canadensis | wood betony | Apr. 20 | Jun. 13 |
| Pedicularis lanceolata | marsh betony | Aug. 24 | Oct. 1 |
| Penstemon calycosus | smooth beard tongue | Jun. 13 | Jul. 26 |
| Penthorum sedoides | ditch stonecrop | Jul. 19 | Oct. 3 |
| Petalostemum purpureum | purple prairie clover | Jul. 3 | Aug. 25 |
| Phlox divaricata | woodland phlox | Apr. 15 | Jun. 8 |
| Phlox glaberrima | marsh phlox | Jun. 22 | Sep. 6 |
| Phlox pilosa | prairie phlox | May 16 | Sep. 5 |
| Phryma leptostachya | lopseed | Jul. 10 | Aug. 12 |
| Physalis heterophylla | clammy ground cherry | Jun. 13 | Sep. 6 |
| Physalis subglabrata | tall ground cherry | Jun. 6 | Sep. 11 |
| Physostegia virginiana | false dragonhead | Aug. 2 | Sep. 11 |
| Phytolacca americana | pokeweed | Jun. 28 | Sep. 16 |
| Pilea pumila | clearweed | Jul. 28 | Oct. 3 |
| Plantago lanceolata | English plantain | May 25 | Sep. 28 |
| Plantago major | pale plantain | Jun. 25 | Sep. 14 |
| Plantago rugelii | common plantain | Jun. 22 | Sep. 23 |
| Podophyllum peltatum | May apple | May 3 | Jun. 8 |
| Pogonia ophioglossoides | snake-mouth orchid | Jun. 18 | Jul. 4 |
| Polanisia graveolens | clammy weed | Jul. 25 | Oct. 6 |
| Polemonium reptans | Jacob's ladder | Apr. 27 | Jun. 1 |
| Polygala cruciata aquilonia | cross milkwort | Jul. 24 | Sep. 25 |
| Polygala polygama obtusata | purple milkwort | Jun. 13 | Aug. 6 |
| Polygala sanguinea | field milkwort | Jun. 22 | Oct. 1 |
| Polygala senega | Seneca snakeroot | May 16 | Jul. 8 |
| Polygala verticillata (vars. isocycla and sphenostachya) | whorled milkwort | Jul. 4 | Sep. 12 |
| Polygonatum canaliculatum | Solomon's seal | May 9 | Jul. 3 |
| Polygonatum pubescens | Solomon's seal | Apr. 15 | Jun. 20 |
| Polygonella articulata | polygonella | Aug. 22 | Nov. 5 |
| Polygonum amphibium stipulaceum | water knotweed | Jun. 27 | Oct. 1 |
| Polygonum aviculare | common knotweed | Jun. 14 | Nov. 6 |
| Polygonum coccineum | water heartsease | Aug. 6 | Sep. 19 |
| Polygonum convolvulus | black bindweed | Jun. 15 | Oct. 1 |
| Polygonum hydropiper | water pepper | Aug. 1 | Oct. 27 |
| Polygonum hydropiperoides | mild water pepper | Aug. 1 | Sep. 2 |
| Polygonum lapathifolium | heartsease | Jun. 29 | Oct. 8 |
| Polygonum pensylvanicum | heartsease | Jun. 14 | Oct. 14 |
| Polygonum persicaria | lady's thumb | May 27 | Nov. 3 |
| Polygonum sagittatum | tear-thumb | Jul. 24 | Sep. 22 |
| Polygonum tenue | slender knotweed | Jul. 31 | Sep. 25 |
| Polymnia canadensis | leafcup | Jun. 25 | Sep. 17 |
| Pontederia cordata | pickerel weed | Jul. 25 | Sep. 14 |
| Potentilla anserina | silverweed | Jun. 5 | Oct. 1 |
| Potentilla argentea | silvery cinquefoil | May 6 | Aug. 29 |
| Potentilla arguta | white cinquefoil | Jun. 30 | Aug. 9 |
| Potentilla fruticosa | shrubby cinquefoil | Jun. 5 | Oct. 1 |
| Potentilla norvegica | false strawberry | Jun. 2 | Oct. 13 |
| Potentilla palustris | marsh cinquefoil | Jun. 8 | Jul. 3 |

| Scientific Name | Common Name | Earliest Date | Latest Date |
|---|---|---|---|
| Potentilla recta | pale cinquefoil | Jun. 3 | Aug. 30 |
| Potentilla simplex | common cinquefoil | May 3 | Jul. 3 |
| Prenanthes alba | white lettuce | Aug. 20 | Oct. 6 |
| Proserpinaca palustris (vars. amblyogona and crebra) | mermaid weed | Jun. 30 | Sep. 6 |
| Prunella vulgaris | carpenter's weed | Jun. 22 | Oct. 27 |
| Prunus pensylvanica | pin cherry | Apr. 7 | Jun. 3 |
| Prunus pumila | sand cherry | Apr. 22 | Jun. 22 |
| Prunus serotina | wild black cherry | May 12 | Jun. 3 |
| Prunus virginiana | choke cherry | Apr. 15 | Jul. 26 |
| Psoralea tenuiflora | psoralea | Jun. 14 | Jul. 9 |
| Ptelea trifoliata | hop tree | May 29 | Jun. 22 |
| Pycnanthemum virginianum | mountain mint | Jul. 24 | Oct. 6 |
| Pyrus ioensis | wild crab | Apr. 15 | Jun. 8 |
| Pyrus melanocarpa | chokeberry | May 6 | Jun. 21 |
| Ranunculus abortivus | small crowfoot | Apr. 7 | Jul. 9 |
| Ranunculus acris | tall buttercup | May 25 | Jul. 9 |
| Ranunculus fascicularis | early crowfoot | Apr. 27 | May 30 |
| Ranunculus flabellaris | yellow water crowfoot | Apr. 27 | Jun. 15 |
| Ranunculus pensylvanicus | bristly crowfoot | Jul. 26 | Sep. 6 |
| Ranunculus recurvatus | hooked crowfoot | May 4 | Jun. 3 |
| Ranunculus septentrionalis | swamp buttercup | Mar. 31 | *Jun. 3 |
| Ratibida pinnata | pale coneflower | Jul. 2 | Sep. 15 |
| Rhexia virginica | meadow beauty | Jul. 25 | Sep. 12 |
| Rhus aromatica | fragrant sumac | May 2 | Jun. 3 |
| Rhus copallina latifolia | shining sumac | Jul. 26 | Aug. 24 |
| Rhus glabra | smooth sumac | Jun. 21 | Jul. 9 |
| Rhus radicans | poison ivy | May 28 | Jun. 26 |
| Rhus typhina | staghorn sumac | Jun. 25 | Jul. 15 |
| Ribes americanum | wild black currant | Apr. 8 | May 30 |
| Ribes cynosbati | prickly gooseberry | Apr. 15 | Jun. 3 |
| Ribes missouriense | wild gooseberry | Mar. 31 | May 27 |
| Rorippa islandica fernaldiana | marsh cress | Jun. 13 | Sep. 2 |
| Rosa blanda | early wild rose | May 25 | Jul. 15 |
| Rosa carolina | pasture rose | May 30 | Aug. 22 |
| Rosa palustris | swamp rose | Jun. 7 | Aug. 19 |
| Rubus allegheniensis | blackberry | May 21 | Jul. 4 |
| Rubus flagellaris | dewberry | May 18 | Jul. 15 |
| Rubus hispidus obovalis | swamp blackberry | May 18 | Aug. 9 |
| Rubus idaeus (vars. canadensis and strigosus) | red raspberry | May 18 | Sep. 3 |
| Rubus occidentalis | black raspberry | May 20 | Jun. 26 |
| Rubus pubescens | dwarf raspberry | Apr. 15 | Jun. 21 |
| Rudbeckia laciniata | tall coneflower | Jul. 29 | Nov. 3 |
| Rudbeckia serotina | black-eyed Susan | Jun. 9 | Oct. 20 |
| Ruellia humilis | hairy ruellia | Jul. 9 | Aug. 24 |
| Rumex acetosella | field sorrel | Apr. 22 | Aug. 1 |
| Rumex altissimus | pale dock | May 8 | *Jul. 9 |
| Rumex crispus | yellow dock | May 30 | Jul. 9 |
| Sabatia angularis | rose gentian | Jul. 25 | Oct. 13 |
| Sagittaria graminea | grass-leaved arrowhead | Jun. 4 | Sep. 12 |
| Sagittaria latifolia | arrowhead | Jul. 26 | Sep. 8 |
| Salsola kali tenuifolia | Russian thistle | Jul. 17 | Oct. 8 |
| Sambucus canadensis | common elder | Jun. 14 | Aug. 25 |
| Sambucus pubens | red-berried elder | Apr. 24 | May 30 |

| Scientific Name | Common Name | Earliest Date | Latest Date |
|---|---|---|---|
| Sanguinaria canadensis | bloodroot | Mar. 30 | May 10 |
| Sanicula gregaria | clustered snakeroot | May 8 | Aug. 12 |
| Sanicula marilandica | black snakeroot | May 8 | Aug. 7 |
| Saponaria officinalis | bouncing Bet | Jun. 11 | Oct. 22 |
| Sassafras albidum | sassafras | Apr. 15 | Jun. 3 |
| Satureja arkansana | low calamint | Jun. 29 | Oct. 1 |
| Saxifraga pensylvanica | swamp saxifrage | May 4 | Jun. 14 |
| Scrophularia lanceolata | figwort | Jun. 2 | Jul. 4 |
| Scrophularia marilandica | figwort | Jul. 19 | Sep. 6 |
| Scutellaria epilobiifolia | marsh skullcap | Jun. 20 | Sep. 25 |
| Scutellaria lateriflora | mad-dog skullcap | Jun. 27 | Sep. 25 |
| Scutellaria parvula | small skullcap | May 29 | Sep. 3 |
| Senecio aureus | golden ragwort | May 11 | Jun. 10 |
| Senecio pauperculus balsamitae | golden ragwort | May 16 | Jul. 3 |
| Silene antirrhina | sleepy catchfly | Jun. 2 | Jul. 29 |
| Silene cserei | bladder campion | Jun. 10 | Oct. 6 |
| Silene stellata | starry campion | Jul. 19 | Oct. 9 |
| Silphium integrifolium | rosin weed | Jul. 2 | Oct. 10 |
| Silphium laciniatum | compass plant | Jul. 2 | Sep. 6 |
| Silphium perfoliatum | cup plant | Jul. 29 | Sep. 6 |
| Silphium terebinthinaceum | prairie dock | Jul. 3 | Sep. 11 |
| Sisymbrium altissimum | tumble mustard | May 21 | Oct. 11 |
| Sisymbrium officinale | hedge mustard | May 30 | Nov. 17 |
| Sisyrinchium albidum | blue-eyed grass | May 12 | Jul. 4 |
| Sium suave | water parsnip | Jul. 17 | Sep. 19 |
| Smilacina racemosa | false spikenard | Apr. 15 | Jun. 21 |
| Smilacina stellata | false Solomon's seal | Apr. 15 | Jun. 10 |
| Smilax ecirrhata | carrion flower | Apr. 28 | Jun. 30 |
| Smilax lasioneura | carrion flower | May 8 | Jul. 26 |
| Solanum americanum | black nightshade | Jul. 21 | Oct. 3 |
| Solanum carolinense | horse nettle | Jun. 21 | Sep. 16 |
| Solanum dulcamara | climbing nightshade | May 26 | Sep. 8 |
| Solidago altissima | tall goldenrod | Jul. 19 | Oct. 22 |
| Solidago caesia | blue-stem goldenrod | Sep. 8 | Oct. 20 |
| Solidago gigantea | smooth goldenrod | Aug. 7 | Sep. 28 |
| Solidago graminifolia | grass-leaved goldenrod | Jul. 29 | Oct. 3 |
| Solidago juncea | early goldenrod | Jul. 24 | Sep. 6 |
| Solidago nemoralis | old-field goldenrod | Aug. 11 | Nov. 3 |
| Solidago racemosa | dune goldenrod | Jul. 14 | Nov. 2 |
| Solidago riddellii | prairie goldenrod | Sep. 6 | Nov. 5 |
| Solidago rigida | stiff goldenrod | Jul. 25 | Oct. 10 |
| Solidago speciosa | showy goldenrod | Jul. 14 | Oct. 27 |
| Solidago ulmifolia | elm-leaved goldenrod | Jul. 29 | Nov. 17 |
| Sonchus arvensis | field sow thistle | Jun. 25 | Oct. 14 |
| Sonchus oleraceus | common sow thistle | Jul. 2 | Oct. 13 |
| Sparganium eurycarpum | bur reed | May 30 | Aug. 24 |
| Spiraea alba | meadowsweet | Jul. 4 | Sep. 13 |
| Spiraea tomentosa rosea | steeple bush | Jul. 31 | Sep. 14 |
| Spiranthes cernua | ladies' tresses | Aug. 22 | Oct. 6 |
| Stachys palustris homotricha | woundwort | Jun. 18 | Sep. 11 |
| Stachys tenuifolia | hedge nettle | Jun. 22 | Aug. 30 |
| Staphylea trifolia | bladdernut | Apr. 17 | May 30 |
| Stellaria longifolia | stitchwort | May 16 | Jul. 15 |
| Stellaria media | common chickweed | Mar. 25 | Nov. 2 |
| Strophostyles helvola | wild bean | Aug. 11 | Sep. 19 |

| Scientific Name | Common Name | Earliest Date | Latest Date |
|---|---|---|---|
| Symplocarpus foetidus | skunk cabbage | Mar. 12 | May 4 |
| Taenidia integerrima | yellow pimpernel | Apr. 27 | Jul. 3 |
| Talinum rugospermum | flame flower | Jun. 20 | Aug. 22 |
| Tanacetum vulgare | tansy | Jul. 31 | Oct. 8 |
| Taraxacum officinale | dandelion | Mar. 30 | Dec. 8 |
| Tephrosia virginiana | goat's rue | Jun. 22 | Jul. 31 |
| Teucrium canadense | wood sage | Jun. 28 | Sep. 6 |
| Thalictrum dasycarpum | purple meadow rue | Jun. 4 | Jul. 9 |
| Thalictrum dioicum | early meadow rue | Apr. 15 | May 30 |
| Thlaspi arvense | penny cress | May 16 | Jun. 27 |
| Tilia americana | basswood | Jun. 13 | Jul. 7 |
| Tofieldia glutinosa | false asphodel | Jun. 30 | Oct. 1 |
| Tovara virginiana | woodland knotweed | Jul. 29 | Sep. 23 |
| Tradescantia ohioensis | spiderwort | May 23 | Oct. 27 |
| Tragopogon major | goat's beard | May 25 | Sep. 26 |
| Tragopogon pratensis | goat's beard | May 22 | Oct. 14 |
| Trientalis borealis | starflower | May 16 | Jun. 14 |
| Trifolium agrarium | hop clover | Jun. 8 | Jul. 26 |
| Trifolium hybridum | Alsike clover | May 18 | Nov. 3 |
| Trifolium pratense | red clover | May 19 | Nov. 5 |
| Trifolium procumbens | low hop clover | Jun. 25 | Aug. 16 |
| Trifolium repens | white clover | May 16 | Oct. 31 |
| Trillium flexipes | declined trillium | Apr. 15 | May 30 |
| Trillium grandiflorum | showy trillium | Apr. 15 | *May 30 |
| Trillium recurvatum | red trillium | Apr. 15 | Jun. 13 |
| Triosteum aurantiacum | horse gentian | Apr. 27 | May 30 |
| Typha angustifolia | narrow-leaved cat-tail | Jun. 25 | Jul. 29 |
| Typha latifolia | broad-leaved cat-tail | Jun. 22 | Jul. 21 |
| Urtica procera | stinging nettle | Jun. 26 | Sep. 16 |
| Utricularia cornuta | horned bladderwort | Jul. 26 | Oct. 13 |
| Utricularia vulgaris | great bladderwort | Jun. 4 | Aug. 30 |
| Uvularia grandiflora | bellwort | Apr. 15 | May 16 |
| Vaccinium angustifolium (vars. laevifolium and nigrum) | low blueberry | Apr. 7 | *Aug. 9 |
| Valeriana ciliata | valerian | Apr. 29 | Jun. 10 |
| Verbascum blattaria | moth mullein | Jun. 13 | Sep. 7 |
| Verbascum thapsus | common mullein | Jun. 22 | Oct. 6 |
| Verbena bracteata | creeping vervain | Jun. 4 | Sep. 5 |
| Verbena hastata | blue vervain | Jul. 3 | Sep. 14 |
| Verbena simplex | narrow-leaved vervain | Jun. 4 | Sep. 12 |
| Verbena stricta | hoary vervain | Jun. 28 | Sep. 22 |
| Verbena urticifolia | white vervain | Jul. 19 | Sep. 12 |
| Vernonia fasciculata | common ironweed | Jul. 19 | Oct. 3 |
| Vernonia missurica | Missouri ironweed | Jul. 29 | Sep. 22 |
| Veronica arvensis | corn speedwell | Apr. 15 | Aug. 30 |
| Veronica peregrina | purslane speedwell | Apr. 29 | Jun. 22 |
| Veronicastrum virginicum | Culver's root | Jun. 22 | Aug. 24 |
| Viburnum acerifolium | maple-leaved arrow-wood | Jun. 1 | Jul. 4 |
| Viburnum lentago | nannyberry | Apr. 28 | Jun. 5 |
| Viburnum trilobum | highbush cranberry | May 12 | Jun. 10 |
| Vicia americana | American vetch | May 16 | Jun. 27 |
| Vicia villosa | hairy vetch | Jun. 8 | Aug. 8 |
| Viola canadensis | Canada violet | Apr. 24 | Jul. 10 |
| Viola conspersa | dog violet | Apr. 7 | May 23 |
| Viola lanceolata | lance-leaved violet | Apr. 27 | Jun. 20 |

| Scientific Name | Common Name | Earliest Date | Latest Date |
|---|---|---|---|
| Viola pallens | Northern white violet | Apr 7 | May 16 |
| Viola papilionacea | common blue violet | Apr 15 | *Jun. 19 |
| Viola pedata lineariloba | bird-foot violet | Apr 22 | *Aug. 6 |
| Viola pedatifida | prairie violet | Apr 29 | Jun. 8 |
| Viola pensylvanica | smooth yellow violet | Apr 8 | May 30 |
| Viola pubescens | downy yellow violet | Apr 28 | Jun. 8 |
| Viola sagittata | arrow-leaved violet | Apr 22 | Jun. 30 |
| Viola sororia | hairy wood violet | Apr 20 | Jun. 8 |
| Vitis riparia | river grape | May 10 | Jun. 27 |
| Xanthium pensylvanicum | cocklebur | Aug. 19 | Sep. 11 |
| Xanthoxylum americanum | prickly ash | Apr 13 | May 21 |
| Zizia aurea | meadow parsnip | Apr 20 | *Jul. 4 |

## Book Review

THE CHROMOSOMES. By M. J. D. White. Methuen and Co. John Wiley and Sons, Inc., New York. 1950. ix+124 pp., frontispiece, 21 text figs., 7 tables. $1.50.

This is a fourth edition of an already well known and highly useful book. Its purpose is to present in brief form, for the use of professional biologists who are not cytologists, the main facts which have been discovered about the chromosomes and their behavior in recent years. Those who have used the previous editions know that it serves its purpose well. It might well be treated as required reading for all teachers of elementary biology, for every cytologist knows that all too many otherwise up-to-date courses in elementary biology include some long-outmoded ideas in cytology. Busy teachers who can justly disclaim adequate time to read such large works as Wilson and Darlington could easily read this little book in an evening.

The principal criticism that might be made is that it has not been revised sufficiently in view of recent work. Thus, his casual dismissal of the spindle fibers takes no account of Schrader's statement that "the reality of the spindle fibers may be regarded as settled" (Mitosis, Columbia University Press, 1944). While most cytologists probably agree with him that "there is no evidence for a 'traction of fibres' at this stage" (anaphase), it is unfortunate to make the statement without reference to Cornman's careful review which led to the opposite conclusion (Am. Nat. 78:410-422). Similarly, the structure of the salivary gland chromosomes is discussed without any reference to the many important papers of Kodani.

The same defect is apparent in the bibliography. The author states that, in so small a book, "it is not necessarily possible to quote 'chapter and verse' for each statement." But the 195 references cited do not include any of date later than 1942. It does not seem unreasonable to expect that a few of the more important recent papers be included, even at the expense of dropping older ones.

This is, in spite of such criticisms, a very useful book, and the reviewer hopes that it will enjoy an even broader circulation than did the preceding editions.—EDWARD O. DODSON, University of Notre Dame, Notre Dame, Indiana.

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